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legume — anatomy & seed

THE LEGUMINOUS SEED

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To divide Leguminosae into two or three families is becoming the custom. Mimosaceae are separated and attached, even, to Rosaceae (through Chrysobalanoideae, it is said). Caesalpiniaceae and Papilionaceae are retained as one or two families in Leguminosae proper. The basis of this re-arrangement is not satisfactorily explained, and the critical tribes, linking the three subfamilies, are unmentioned, namely Parkieae and Dimorphandreae linking Mimosoideae and Caesalpinioideae, and Swartziae, Cadieae and Sophoreae linking Caesalpinioideae with Papilionatae. Now, seed-structure introduces new criteria which distinguish the Leguminous seed, on the one hand, from the Rosouaces, and which link the Mimosoid and Caesalpinioid seeds on the other hand, distinguishing the Papilionaceous seed as their specialization and indicating the Swartzieae as a fourth subfamily linking the other three, as De Candolle proposed in 1825 (Prodromus). The facts are more or less known, but unsystematized. My intention is to present the main family and subfamily characters, so far as can be judged from published accounts and from my own researches. During 1943-1945 in Singapore, I studied in detail 71 species, representing 45 genera (Mimosoideae 8 gen., 10 spp.; Caesalpinioideae 15 gen., 32 spp.; Papilionatae 21 gen., 28 spp.; Swartzioideae 1 sp.). My impression is that seed-structure has fundamental importance in classification, perhaps even to generic rank in Papilionatae.

Abbreviations

The same abbreviations have been used for lettering of the figures as in my paper on the Annonaceous seed, with certain additions necessitated on account of the more complicated Leguminous seed. The full list is as follows:

aer.	aerenchyma
ar.	aril
arp.	antiraphe
c. pal.	counter-palisade
ch.	chalaza
cot.	cotyledon
cu.	cuticle
em.	embryo
en.	endosperm
ent.	endostome
ext.	exostome
f.	funicle
h.	hilum
h. gl.	hour-glass cells
i.e.	external integument
i.i.	internal integument
l.	lens
l.l.	linea lucida
m.	micropyle
mes.	mesophyll (of *i.e.*)
n.	nucellus
p.	plumule
pal.	palisade
pl.	pleurogram
r.	radicle
rp.	raphe
r.v.b.	recurrent *v.b.*
s.h.	subhilar tissue
s.m.	mucilage-stratum
st.	stellate cells
t.b.	tracheid bar
v.b.	vascular bundle

In all the diagrams I have used a uniform method for indicating palisade, hour-glass cells, vascular tissue (dotted), tracheid bar (hatched), aerenchyma, stellate cells, and so on. Air-spaces are shown in black.

The Leguminous Ovule

The sessile or shortly stalked ovule is anatropous or campylotropous. The outer integument consists of 3-5 cell-rows on the sides of the ovule, and the inner integument of 2-3. The nucellus is well-developed, but consumed after fertilization by the embryo sac. As oddities, I have observed that the endostome in *Amherstia*

(Caesalp.) is red from anthocyanin at the time of fertilization: that in *Cassia occidentalis* (Caesalp.) the endostome, chalaza and funicle become deep pink after fertilization, the colour persisting only in the funicle; and that in *Cassia hirsuta* the chalaza becomes dark brown after fertilization. In other plants that I have studied, the ovule is colourless but, in all cases after fertilization, it becomes deep green because of the occurrence of chlorophyll in the outer integument and, subsequently, in the embryo.

The first change in the ovules after fertilization is the lengthening of the funicle and, where present, the inception of the aril or arillode. The inner integument enlarges by anticlinal divisions without multiplication or differentiation of its cell rows: at maturity it is more or less obliterated. The outer integument, in contrast, becomes complicated, and it is with its structural developments that I am concerned.

General Features of the Leguminous Seed

The seed is generally of medium or large size, more or less compressed and exalbuminous, with large embryo and hard, dry, smooth testa. Distinctly albuminous seeds occur in all three subfamilies. Two microscopic characters distinguish the Leguminous testa, as emphasized by Pitot (1935a, b): (a) the *external palisade*, developed from the outer epidermis of the outer integument, and (b) the *hour-glass cells*, developed from the outer hypodermis of the outer integument and, in some cases, from its inner epidermis.

Any microscopic particle with these features is, apparently, identifiable as Leguminous (Figs. 1, 2).

A full description of the testa requires mention of several other features, variously present in genera or species:

1. Cuticle (the *stratum externum* of Italian authors).

2. Palisade of columnar, outer epidermal cells (the *Malpighian cells* of Italian authors; also called 'macrosclereids' and 'osteosclereids'), always in a single row and, typically, with four characteristics: (a) a mucilage-stratum (the *stratum mucilaginosum* of Italian authors), representing the periclinal wall between the cell-lumen and the cuticle,

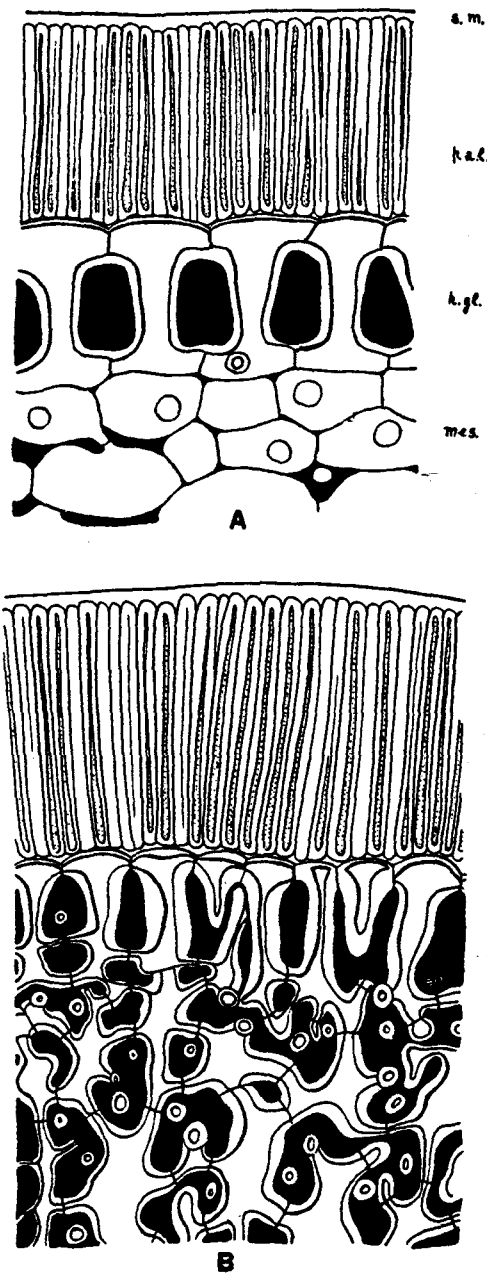

FIG. 1 — *Mucuna utilis* (Papilionaceae). A, outer layer of the testa on the side of the seed. B, same from the subhilar region. ×225.

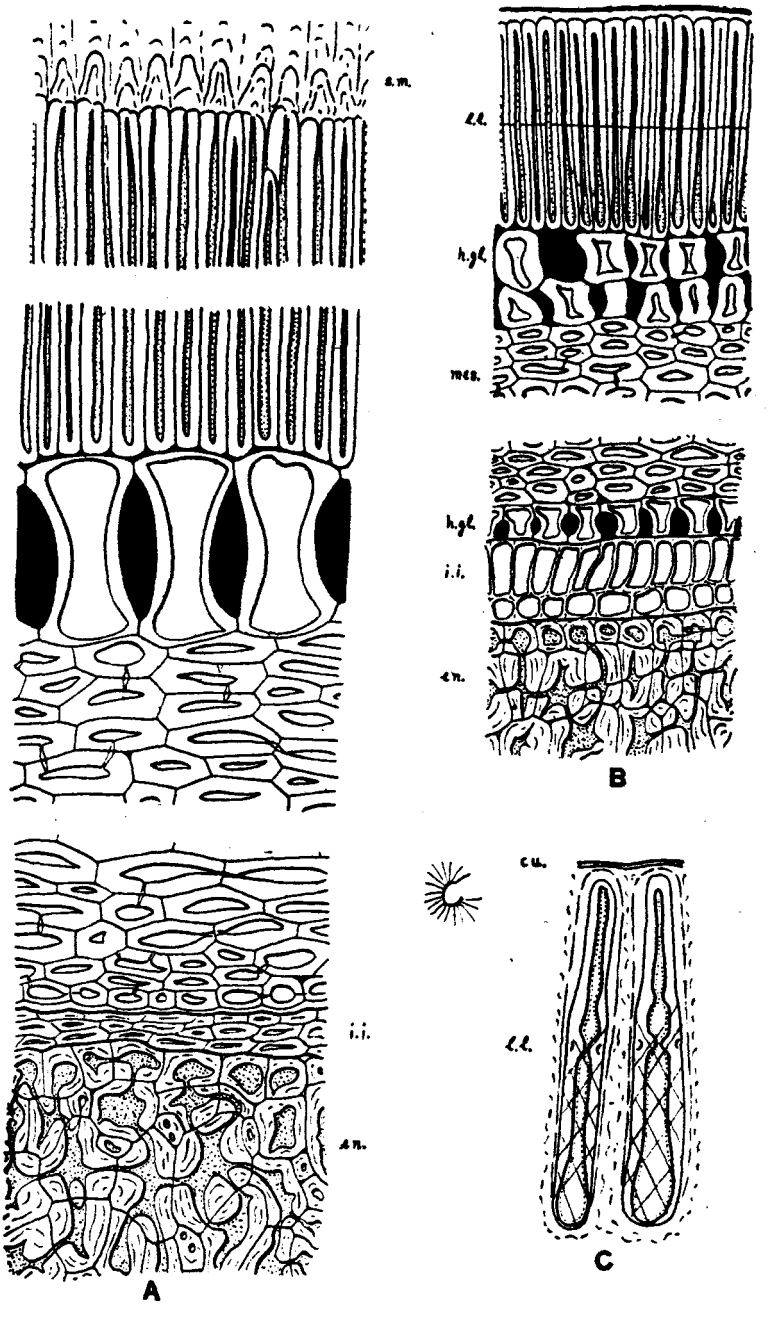

FIG. 2 — A, *Erythrophloeum guineense* (Caesalp.), part of the testa from the side of the seed (the outer part of palisade not shown, cf. Fig. 3). B, *Delonix regia* (Caesalp.), similar section. C, *Bauhinia fassoglensis* (Caesalp.), palisade cells swollen in water, with a sketch to show these cells separating and curling back on the cuticle. ×225.

often with caps or cones as the layering of the wall on thickening; (b) an outer rod-like stratum with narrow cell-lumen; (c) an inner columnar stratum with wider, nucleate, cell-lumen; (d) a *linea lucida* (or optical line) separating the layers *c* and *b*.

3. Hypodermal hour-glass cells.
4. Mesophyll.
5. Inner epidermal hour-glass cells.
6. Vascular supply.
7. Structural modifications in the raphe-antiraphe compared with the sides of the seeds.
8. Subhilar tissue.

CUTICLE — This layer is always thin and smooth. The rather thick, tough or woody, pellicle or shell of the testa, often separable from the immature seed, consists of the outer ends of the palisade-cells.

PALISADE — The prismatic, thick-walled, contiguous cells, more or less hexagonal in cross-section, which make the palisade are derived from the outer epidermis of the outer integument. This simple fact must be emphasized, because in other families the palisade is shifted gradually inward in its origin until the outer epidermis of the inner integument may be the layer to differentiate. The layer begins to develop when the seed is nearly full grown. In some cases the palisade-cells differentiate simultaneously over the whole seed, but in other cases there is a gradation, as in *Delonix* (Caesalp.) in which differentiation proceeds from the hilum to the chalaza, or a diversion, as in Mimosoid seeds with pleurogram (*vide infra*) where the palisade apparently differentiates from the sides of the seed and from the raphe-antiraphe independently. Young palisade-cells have colourless, aqueous contents and their walls thicken from the outer end inwards, often with oblique pitting: in *Caesalpinia pulcherrima* the inner ends of the cells do not thicken, but dilate into the form of hour-glass cells.

MUCILAGE-STRATUM — The outer periclinal walls of the palisade-cells become more or less gelatinous, and often show successive thickening. The feature is well marked on the sides of the seed of *Erythrophloeum guineense* (Dimorphandreae, Caesalp.), as shown in Fig. 3. The outer, firmer, ends of the cell-walls project as cones or caps into the mucilage-stratum, the formation of which takes place by periclinal zones of hydration or vacuolation in the outer walls. In *Erythrophloeum* the result is a plump seed before it dries off, with thickly gelatinous sides and a median depressed band along the raphe-antiraphe where the mucilage-stratum is poorly developed (Figs. 6, 7). This layer is fairly well-formed in *Parkia* and *Adenanthera* (both Mimosoid) (Figs. 16, 17), and contains in *Adenanthera* most of the red, water-soluble pigment of its seed. In *Delonix* and many others the layer is absent or so slight as to be scarcely noticeable (Fig. 2). In *Bauhinia fassoglensis* each palisade-cell is surrounded by a mucilage-sheath, derived from the primary layer of the wall (Fig. 2).

LINEA LUCIDA — This optical effect gives the false impression that the palisade consists of two layers of cells, for it occurs only where there is the differentiation of the palisade-cells into outer and inner parts with difference in cell-lumen. In longitudinal section of the palisade-cell, the *linea lucida* shows as a bright spot in the cell-wall at the junction of the two parts: in intact or surface view it shows as a dark line simulating the division of the cell. The relation of the *linea lucida* to the palisade-cell is well shown in *Erythrophloeum* (Fig. 3): the upper figure, A, shows the palisade on the side of the seed adjoining the raphe, with the palisade-cells and their mucilage-stratum shortening toward the low palisade on the raphe, B: at the hilum, C, the short palisade has the *linea lucida* (absent from the rest of the seed) in the position of the firm outer ends of the palisade-cells of the raphe. In many leguminous seeds there is no *linea lucida* except in the hilum-palisade.

The hardness and impermeability of the dried testa is caused mainly by the contraction of the walls of the palisade-cells as the seed ripens. When dried, the palisade may be almost impossible to section, but a trace of water on a fractured surface enables the razor to glide through. Thus, as soon as the surface of the testa is cracked, the palisade swells and the seed can germinate. [In *Melilotus alba*, according to Hamly (1932), the outer periclinal wall is more or less suberized.]

HOUR-GLASS CELLS — These cells have a position and a form intermediate between the palisade and the stellate-celled mesophyll, and so they indicate the interaction of evocators, or tissue-factors, in the developing seed. They lie between the palisade and mesophyll as the hypodermal layer, or they occupy the position of the inner epidermis of the outer integument. The inner ends of the palisade-cells may even themselves come into the sphere of the mesophyll and be modified into stellate-armed hour-glass cells. The name refers to the more extreme form. Generally the cells are columnar, but slightly waisted, and with expanded stellate ends, as if they were I-girders of revolution with stellate arms in place of end-discs. Between them are wide air-spaces, and, if the cells are tall, the tissue looks like a pillared crypt. Usually the cells are in a single layer, but there are two rows in the outer hypodermis of *Delonix* (Fig. 2), and in the Papilionaceous *Canavalia*, *Ormosia* and *Vicia* there may be 2-6 rows near the hilum. In some cases the inner ends of the cells are irregularly stellate, as if affected by the mesophyll-factors (Fig. 1). In other seeds there are no hour-glass cells or they are so rudimentary as to be indistinguishable, as in *Parkia*, *Adenanthera*,

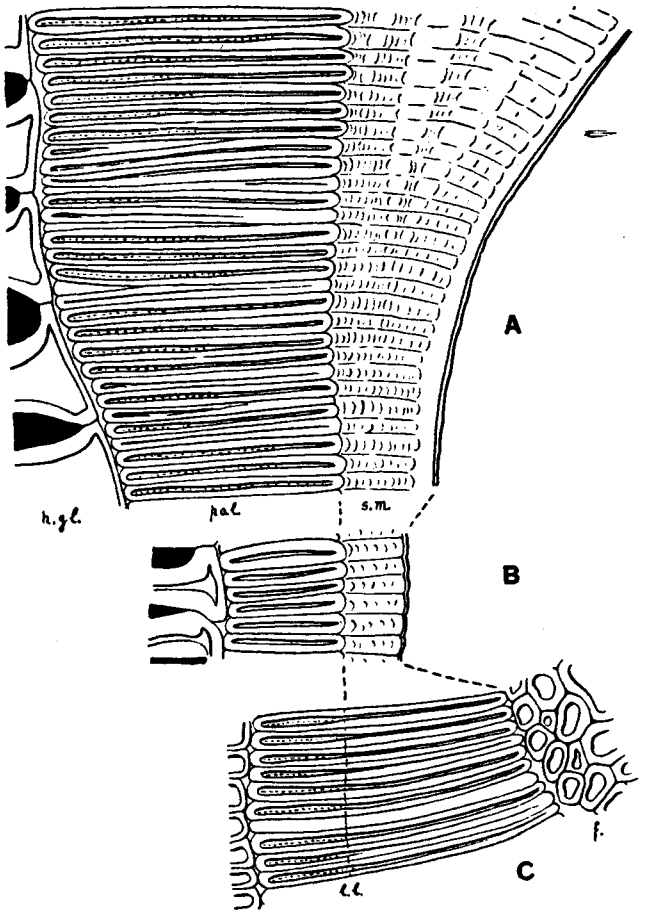

FIG. 3 — *Erythrophloeum guineense* (Caesalp.). A, transverse section of the palisade at the junction of the side of the testa with the raphe. B, at the raphe. C, at the hilum. ×225.

Bauhinia and *Caesalpinia*. The inner hour-glass cells are usually less defined, more often absent, but well-developed in *Cassia*.

MESOPHYLL. — This tissue forms the body of the testa and develops from the middle cell-layer, or cell-layers, of the outer integument. It becomes a chlorophyllous aerenchyma consisting, typically, of outer and inner layers of stellate cells separated by ordinary large-celled paren-

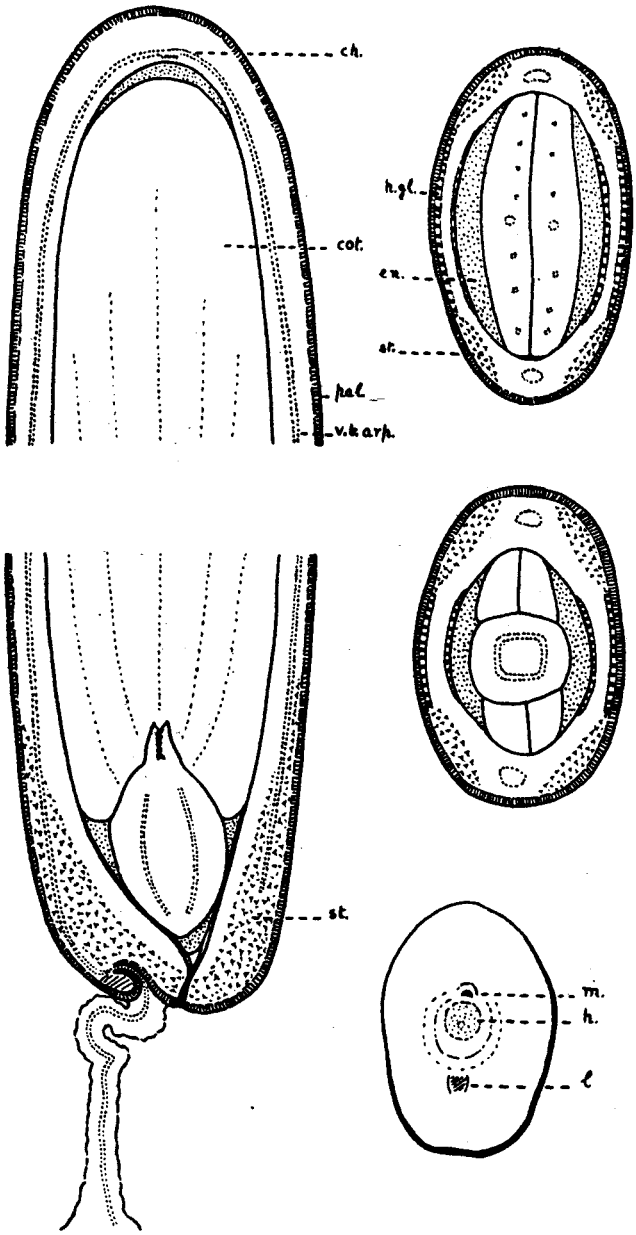

FIG. 4 — *Delonix regia* (Caesalp.). Seed in median longitudinal section, with two transverse sections, and the hilum (lower right) in surface view. ×6.

chyma. In some cases there are no stellate cells, as in *Erythrophloeum*, *Delonix*, *Bauhinia* spp., and *Cassia* spp. On ripening of the seed, the tissue becomes thick-walled and the cells contract into angular or condensed shapes, difficult to make out without reference to the unripened seed.

HILUM — When the seed breaks from the funicle, an abscis-layer is developed, so that the hilum is sharply defined. The abscis-layer is merely a continuation of the palisade of the outer integument across the base of the seed, though pierced by the v.b.: it nearly always has the *linea lucida*.

SUBHILAR TISSUE — Between the hilum and the endosperm the outer integument is thickened and this subhilar tissue consists generally of stellate-celled aerenchyma. In Mimosoid-Caesalpinioid seeds there is often a hard, compact tissue of 2-6 (or more) rows of very thick-walled, pitted, contiguous cells immediately below the hilum and serving as a strut against the contraction of the testa on to the radicle (cf. the subhilar plug of the Annonaceous seed). In the Papilionatae the subhilar tissue contains the enigmatic tracheid bar (*vide infra*). On the raphe-side of the hilum there is often seen in surface view a horny patch which indicates a lens-shaped mass of contiguous cells with very thick, highly refractive walls and, often, dense contents: it is a local differentiation of the mesophyll, but without apparent significance. In Mimosoid-Caesalpinioid seeds the v.b. often takes a characteristic bend round or through the lens. In *Bauhinia* the lens is on the micropylar side of the hilum. In the Papilionaceous seed it may be single or, apparently, the 'corpora geminata' of Italian authors.

RAPHE-ANTIRAPHE — In this median longitudinal band of the testa all the

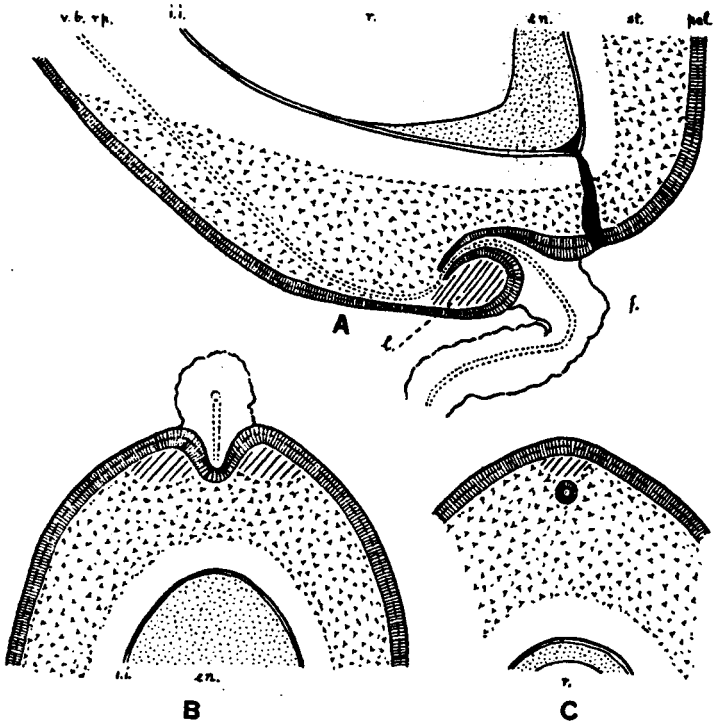

FIG. 5 — *Delonix regia* (Caesalp.). A, median longitudinal section of the hilar region. B, transmedian longitudinal section of the hilum. C, transmedian tangential section through the beginning of the raphe, the v.b. enclosed in the palisade-tube. ×15.

cells may be variously modified, in ways characteristic of genera or species. Hour-glass cells may be missing: the mesophyll is rarely stellate: the mucilage-stratum may be missing, or feebly developed: the position of the *linea lucida* may be altered. In some cases such modifications occur only at the beginning of the raphe. The chalaza, separating the raphe from the antiraphe, has little

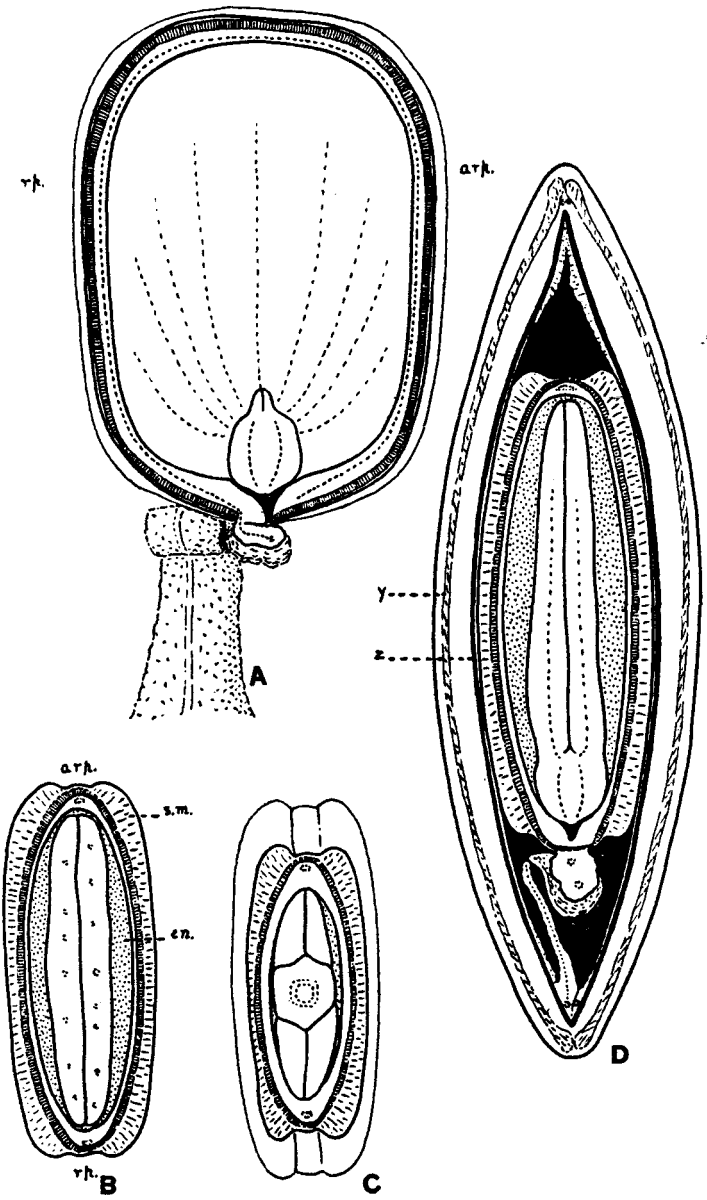

FIG. 6 — *Erythrophloeum guineense* (Casesalp.). A, median longitudinal section of the seed with funicle. B, C, transverse sections. D, transmedian longitudinal section of the seed in the legume; *y*, woody layer of the mesocarp; *z*, woody layer of endocarp (as a heavy line). ×3.

distinction other than a slight thickening or spreading of the v.b.

Mimosoid-Caesalpinioid Seeds

The seeds of these two subfamilies have the following peculiarities distinguishing them from the Papilionaceous:

1. Symmetrical shape, the chalaza being at the opposite end from the hilum, and the raphe and antiraphe being equal. (*Bauhinia* spp., which lack the post-chalazal part of the v.b., have asymmetric seeds, Figs. 10, 13.)

2. The v.b. extends in a single hoop in the raphe-antiraphe round the whole

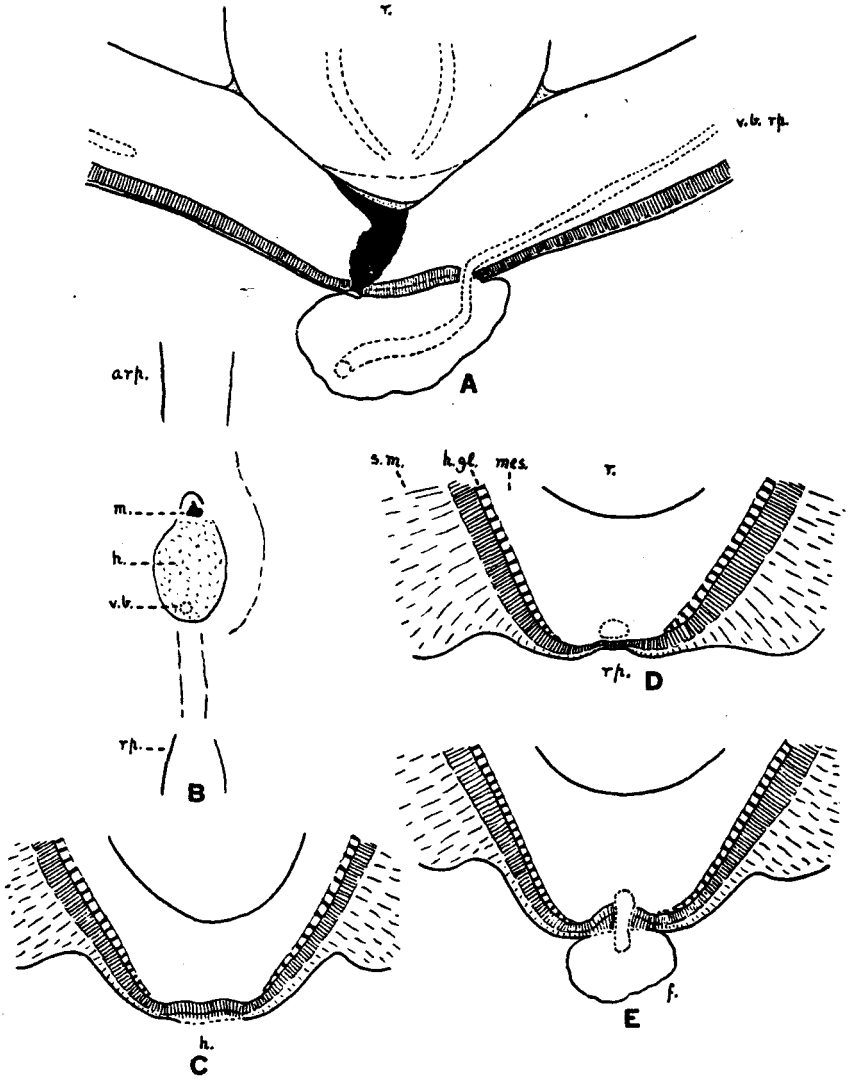

FIG. 7 — *Erythrophloeum guineense* (Caesalp.). A, median longitudinal section through the hilum. B, the hilum in surface view. C, transmedian longitudinal section of the hilum, with the funicle detached, on the micropylar side. D, the same on the raphe-side. E, the same through the central part. ×15.

seed (except those species of *Bauhinia* mentioned in the preceding paragraph).

3. Small, round or shortly oblong, hilum closed by a single palisade without median groove (except Amherstieae-Cynometreae which have a short, slit-like hilum without palisade).

4. Long funicle (except Amherstieae-Cynometreae without arillode, *Bauhinia* pr. p., *Caesalpinia*, *Peltophorum*).

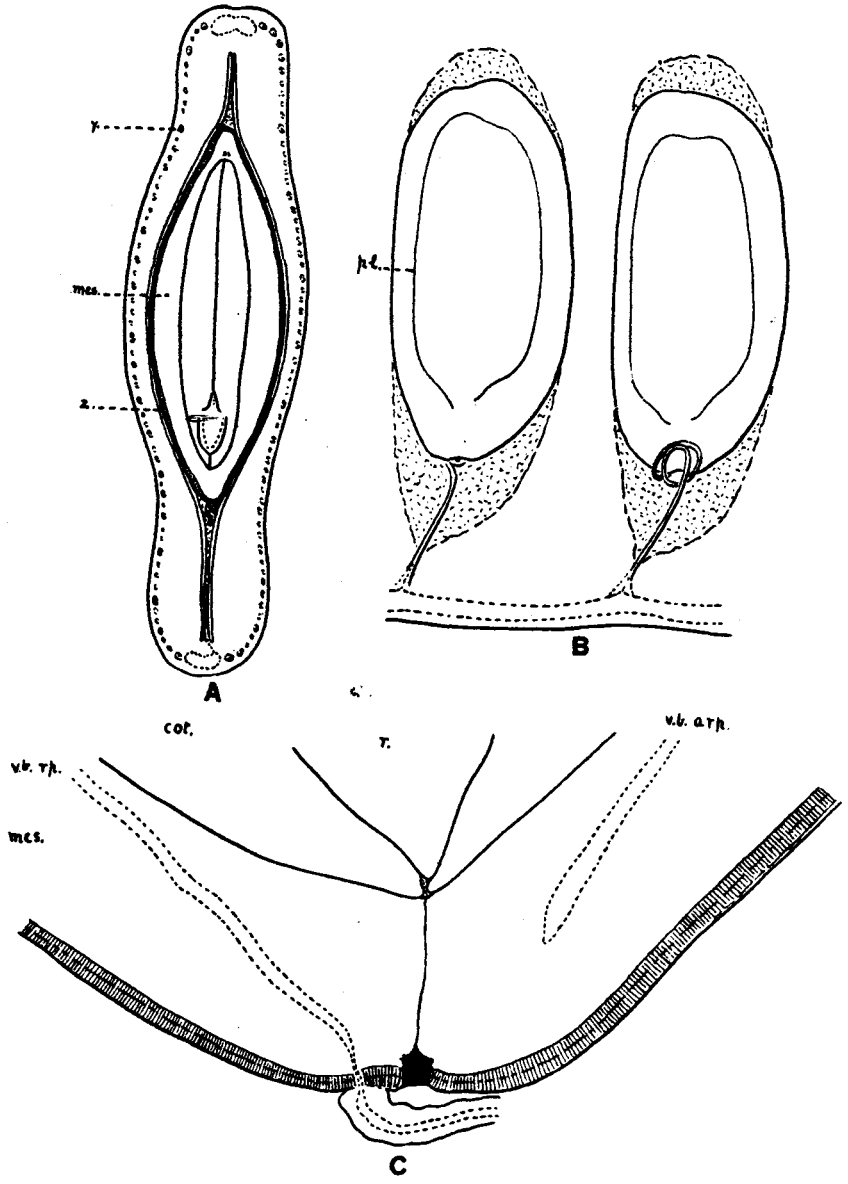

FIG. 8 — *Parkia javanica* (Mimosoideae). A, transmedian longitudinal section of the seed. B, two seeds in surface view, in the legume. ×2. C, a median longitudinal section of the hilum. ×15. (*y*, the layer of fibres and stone-cells in the outer mesocarp; *z*, the endocarp.)

5. Symmetrical embryo with straight, short, thick, radicle (except *Bauhinia* spp., and *Petalostyles* of the Cassieae).

6. Thin-walled cotyledon-cells without starch-grains or only a few (except Amherstieae-Cynometreae with thick-walled, horny, cotyledon-cells, often with amyloid cellulose and starch-grains).

ENDOSPERM — The following genera or tribes have distinctly albuminous seeds, though traces of endosperm round the radicle occur in most cases (as in Papilionatae):

Mimosoideae — Adenanthereae and Eu-Mimoseae (at least in the chalazal half of the seed).

Caesalpinioideae — (Caesalpinieae-Sclerolobeae) *Caesalpinia* pr. p. (e.g. in *C. pulcherrima*, but not in *C. sappan*), *Peltophorum*, *Delonix*, *Gymnocladus*, *Gleditschia*, *Schizolobium*, *Cercidium*, *Parkinsonia*; Cassieae: *Bauhinia* pr. p. (Dimorphandreae) *Erythrophloeum* (? except *E. densiflorum*), *Dimorphandra*.

The cells of the endosperm have thick, deeply pitted walls with stellate lumen.

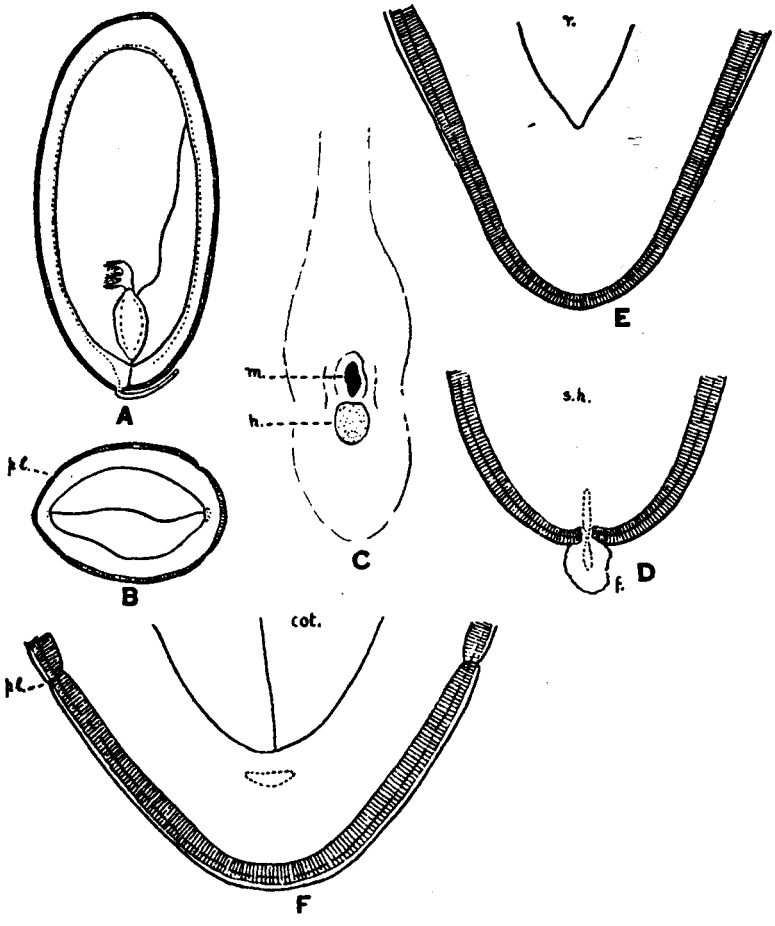

FIG. 9 — *Parkia javanica* (Mimosoideae). A, B, seeds in median longitudinal and transverse section respectively. ×2. C, the hilum in surface view. ×15. D, transmedian longitudinal section of the hilum. E, transmedian longitudinal section of the antiraphe-side of the hilum. F, t.s. of raphe. ×15.

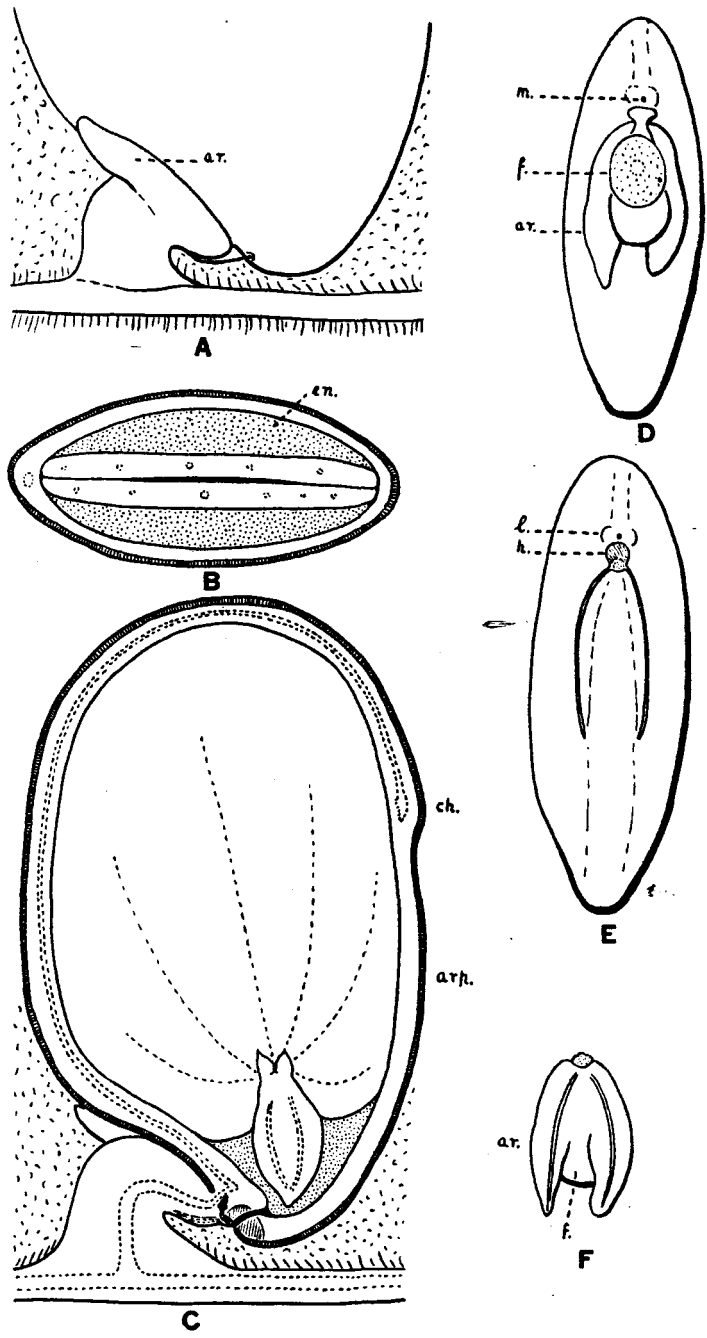

FIG. 10 — *Bauhinia picta* (Caesalp.). A, lower half of the seed in surface view. B, seed in t.s. C, seed in median longitudinal section. D, hilum with funicle attached. E, hilum with funicle detached. F, funicle with aril-lobes detached from the hilum. ×6.

The walls swell strongly in water, when the tissue resembles the medulla of an alga.

PLEUROGRAM — By this name I call the hoop-like or heart-shaped line characteristic of many Mimosoid seeds. It is a fine groove in the testa on each side of the seed, following the curve of the raphe-antiraphe, but always open at the hilar end (Figs. 8, 16, 17).

In *Adenanthera pavonina*, or in *Pithecellobium dulce*, the pleurogram is seen in section as a microscopic break in the palisade with a slight ridge of mesophyll immediately internal (Fig. 17) : the testa has the same relatively simple structure on either side of the break. In the developing seed the break arises soon after the epidermal cells have ceased dividing and have begun to elongate into palisade-

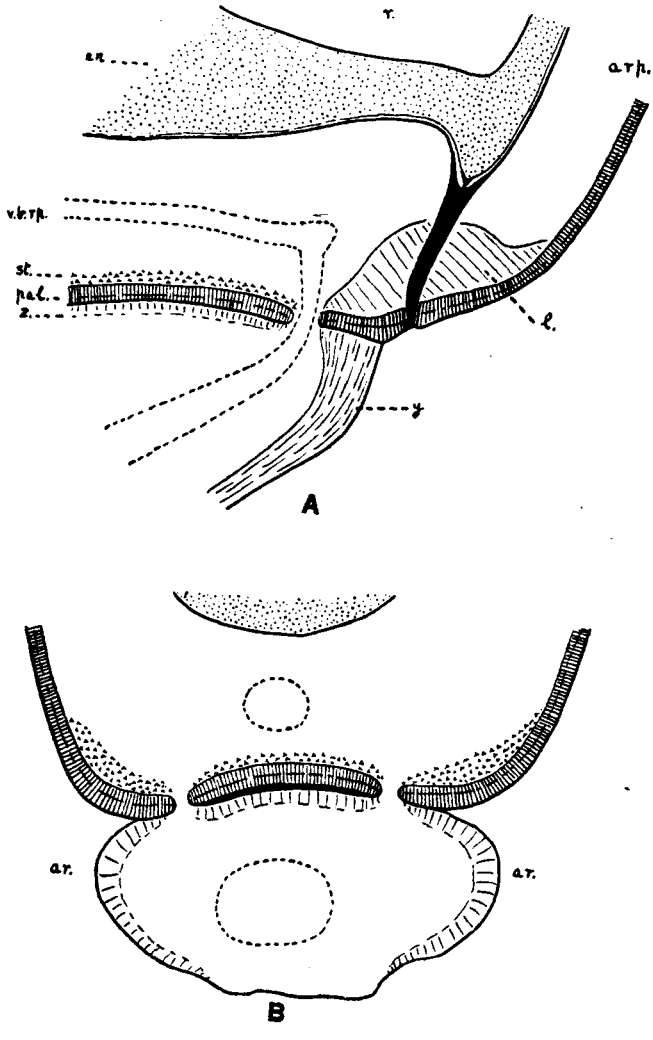

FIG. 11 — *Bauhinia picta* (Caesalp.). A, median longitudinal section of the hilum with the funicle attached. B, transmedian longitudinal section of the hilum to show the attachment of the aril-lobes. ×30. (*v*, the horny tissue of the funicle; *z*, the epidermis of the funicle-head.)

cells. The pleurogram then appears as a slight depression on the outside of the outer integument with shorter palisade-cells on either side and with the mesophyll-ridge incipient (Fig. 17). It looks as if the palisade differentiates from two sources, the raphe-antiraphe and the sides of the seed (plus the hilum), so that where these processes meet and interfere the groove results, and the pleurogram is inscribed as a morphogenetic symbol. Similarly one may note the limited origin of the aril, as an indication of morphogenetic centres in the developing seed.

In *Parkia* (Fig. 16) the pleurogram is a similar interruption of the palisade with raised mesophyll, but, whereas there are no hour-glass cells in the testa generally, they are distinctly, if irregularly, formed in this ridge of mesophyll.

In a species of *Albizzia* (Fig. 17) the mesophyll is further altered. The single layer of hour-glass cells in the testa gives place over the broad low mesophyll-ridge

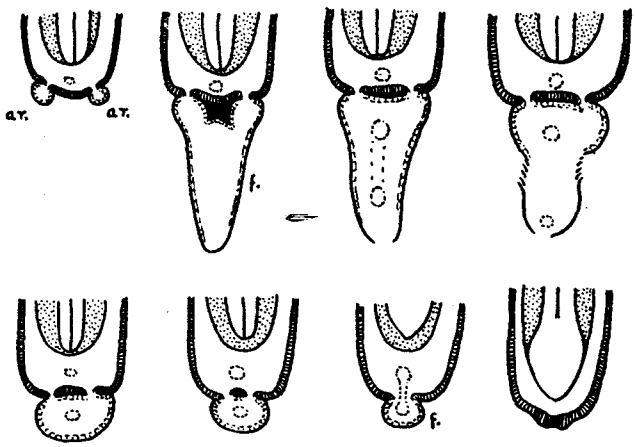

FIG. 12 — *Bauhinia picta* (Caesalp.). Successive transmedian longitudinal sections of the hilum, to show the attachment of the aril-lobes, from the raphe-side (upper left) to the micropyle (lower right). ×6.

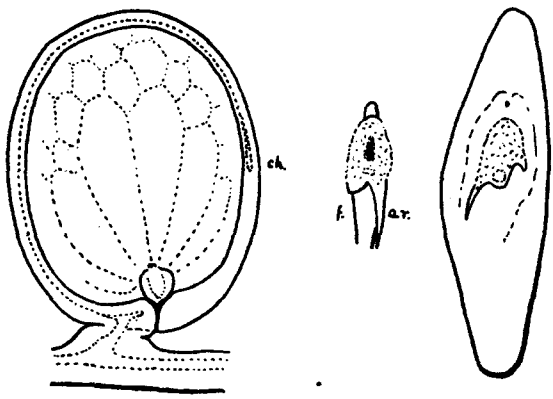

FIG. 13 — *Bauhinia purpurea* (Caesalp.). The seed in median longitudinal section: ×3; the head of the funicle, showing the one aril-lobe, and the hilum with the funicle detached. ×6.

to 3-4 layers, more or less well-formed, and there is an internal bulge of the mesophyll indenting the cotyledons.

The seeds of *Leucaena glauca* and *Acacia auriculaeformis* have the outer row of hour-glass cells, as in *Albizzia*, but their pleurogram is merely a fine groove without modification of the mesophyll. The rather similar seed of *Mimosa pudica* (Fig. 17) has the hour-glass cells below the pleurogram slightly enlarged.

The Caesalpinioideae do not have this linear pleurogram, but on the sides of the seeds of many species of *Cassia* there is an analogous modification as a slightly raised, or depressed, patch of testa wholly circumscribed by a sharp, though not depressed, boundary : I will defer detailed description to another paper. The only other indication of a pleurogram that I have met in this subfamily is in *Delonix* :

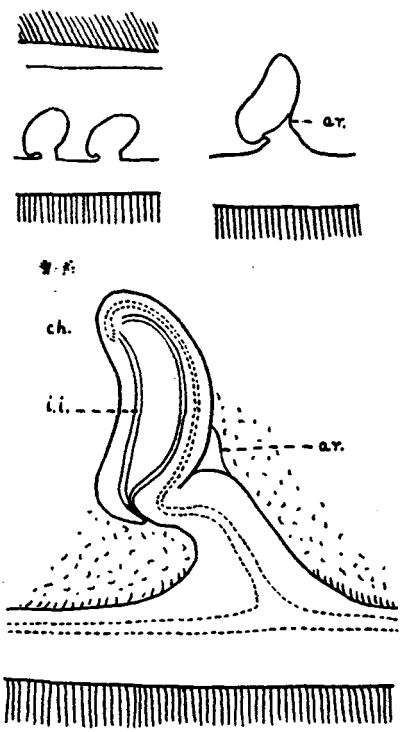

FIG. 14 — *Bauhinia picta* (Caesalp.). Ovules at the time of pollination and shortly after fertilization to show the early origin of the aril-lobes and the asymmetric growth of the raphe. ×15.

its seed has no external marking other than the four pale longitudinal bands — two on each side — marking the four multiseriate rows of hour-glass cells at the junction of the raphe-antiraphe and the sides of the seed : in this seed the palisade develops from the hilum towards the chalaza and not as in *Adenanthera* and *Parkia*.

Whether the presence of the pleurogram is a generic or tribal feature of the Mimosoideae, I have not ascertained.

VASCULAR SUPPLY — The single slender vascular bundle lies in the mesophyll as a hoop stretching from the funicle round the seed almost to the micropyle. In some species of Bauhinia, only, there is no post-chalazal extension : among these species may be seen also a slight projection from the v.b. into the subhilar tissue (Figs. 11, 13, 15). The vascular bundle may take a characteristic course on immediate entry into the raphe. In *Erythrophloeum*, *Adenanthera*, *Leucaena* and *Sindora* (Caesalp.), it passes gradually and obliquely to the inner part of the mesophyll. In *Parkia* and *Tamarindus* (Caesalp.) it passes quickly and suddenly to the inner part of the mesophyll. In *Delonix* and, to a less degree, in *Caesalpinia pulcherrima* and *C. sappan*, the first part of the v.b. is enclosed in a tube of palisade, invaginated, as it were, from the hilum (Figs. 4, 5).

The slenderness and lack of ramification of the v.b. may account, in part, for the slowness in growth of the Mimosoid-Caesalpinioid seeds (3-10 months) compared with the Papilionaceous (1-3 months).

Papilionaceous Seeds

The microscopic structure of the hilum appears to be the most characteristic feature of this subfamily. The Papilionaceous corolla merges into that of the sub-actinomorphic Caesalpinioideae in several aberrant genera of Sophoreae, as well as in the Swartzioideae, but not, so far as known, the hilum. Typical of the Papilionatae are the following peculiarities:

1. Hilum often relatively large, round, oblong or extended, with median groove.

2. Tracheid bar in the subhilar tissue.
3. Counter-palisade on the hilum.
4. Rim-aril surrounding the head of the funicle and generally adherent to the hilum.
5. Two recurrent v.b. in the subhilar tissue.
6. Vascular supply generally without post-chalazal extension, often elaborated from the raphe and the recurrent v.b.
7. Asymmetry about the transmedian longitudinal plane, the raphe shorter than the antiraphe (ovule campylotropous).
8. Short funicle.
9. Exalbuminous (a few exceptions as *Crotalaria*, Text-Fig. 19, and *Indigofera*).
10. Radicle generally elongate and curved.
11. Cotyledon cells generally thin-walled.

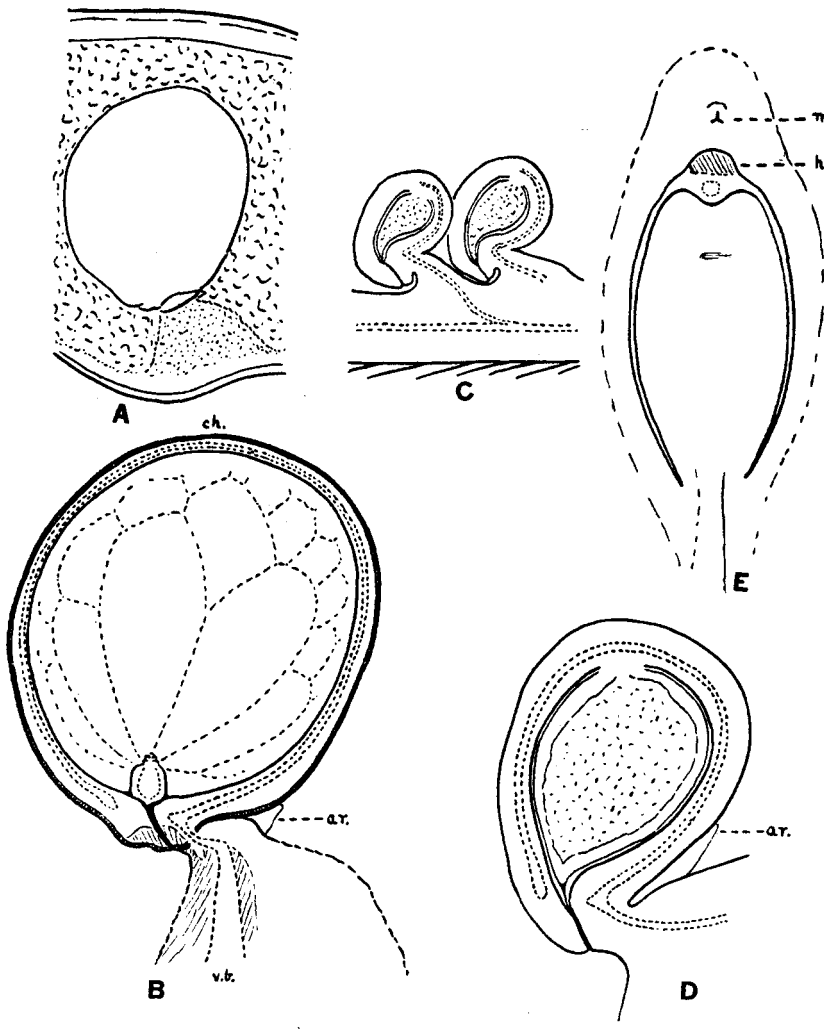

FIG. 15 — *Bauhinia fassoglensis* (Caesalp.). A, mature seed in the legume. ×1. B, seed in median longitudinal section. ×2. C, ovules at the time of pollination. D, the young seed showing the symmetrical growth with the post-chalazal v.b. E, hilum with the funicle detached. ×6.

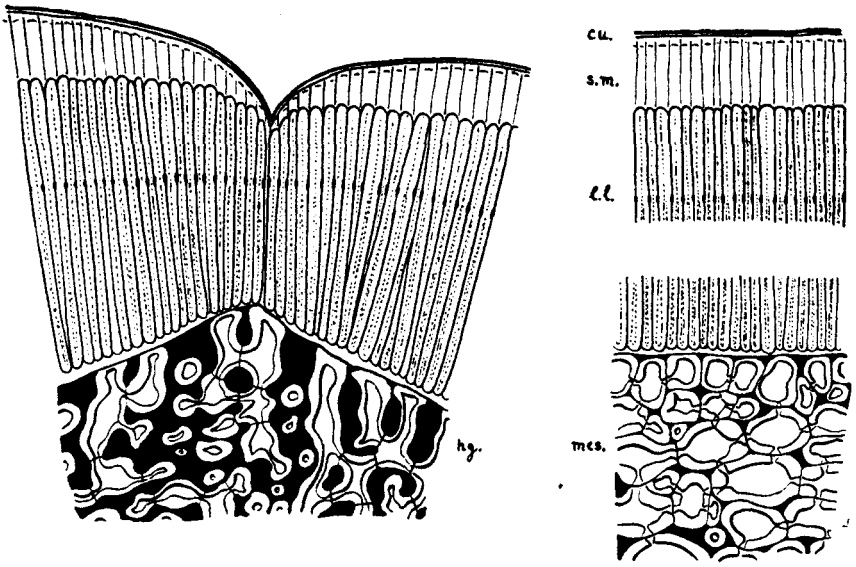

FIG. 16 — *Parkia javanica* (Mimosoideae). Transverse sections of the palisade at the pleurogram (left) and in the central part of the side of the seed (right). ×225.

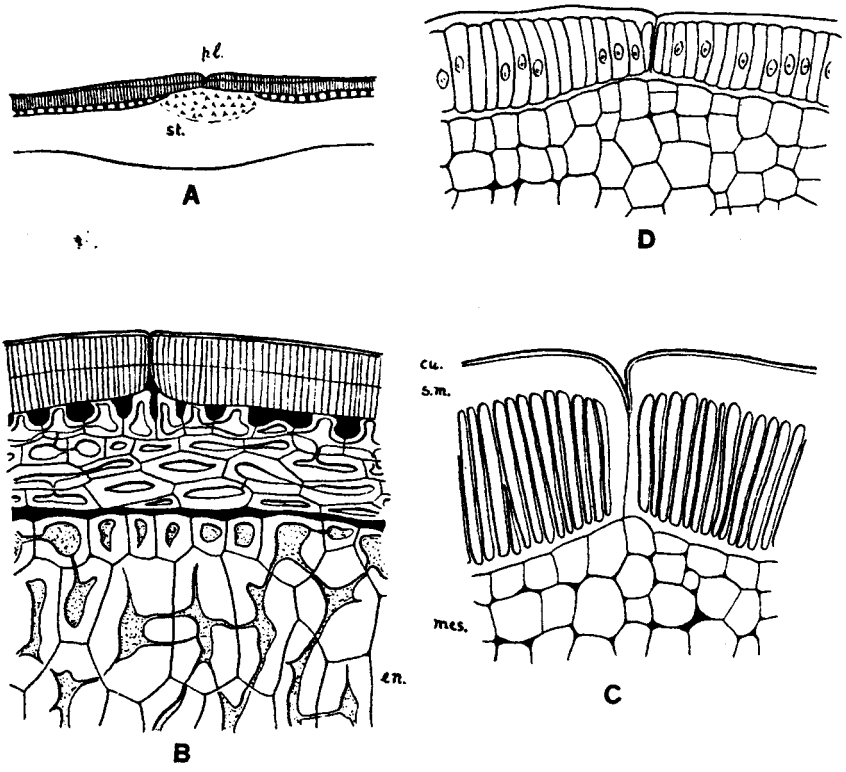

FIG. 17 — Mimosoid seeds showing the pleurogram in transverse section. A, *Albizzia* sp. (aff. *A. odoratissima*). ×40. B, *Mimosa pudica*. ×225. C, *Adenanthera pavonina*, showing the mature pleurogram. D, same, showing its inception in the young palisade. ×225.

THE BEAN-HILUM — The structure of the bean-hilum has long been known, mainly through the work of Italian botanists from Malpighi onwards, but it has found no place in general or systematic botany. It is one of the elaborate examples of plant-structure and has clearly a long evolutionary history. The construction can be gathered most readily from the figure of *Desmodium triflorum* (see Corner, 1949a) in which the entire hilum is small enough to be figured in detail. The head of the funicle is expanded into a bordered disc fitting like a stopper into the depression of the hilum. The border is the *rim-aril*, which is at once a rudiment and a vestige — a rudiment because it stops growing in the initial stages of the development of a large aril (as that of *Swartzia pinnata*, Fig. 22), and a vestige according to the durian-theory: it is the 'terzo strato di cellule malpighiane' of Italian authors, but it does not have Malpighian or palisade-cells. The palisade of the testa covers the face of the hilum, as in Mimosoid-Caesalpinioid seeds, but the adjacent layer of cells in the head of the funicle is also transformed into a palisade-layer, and the cell-walls between the two

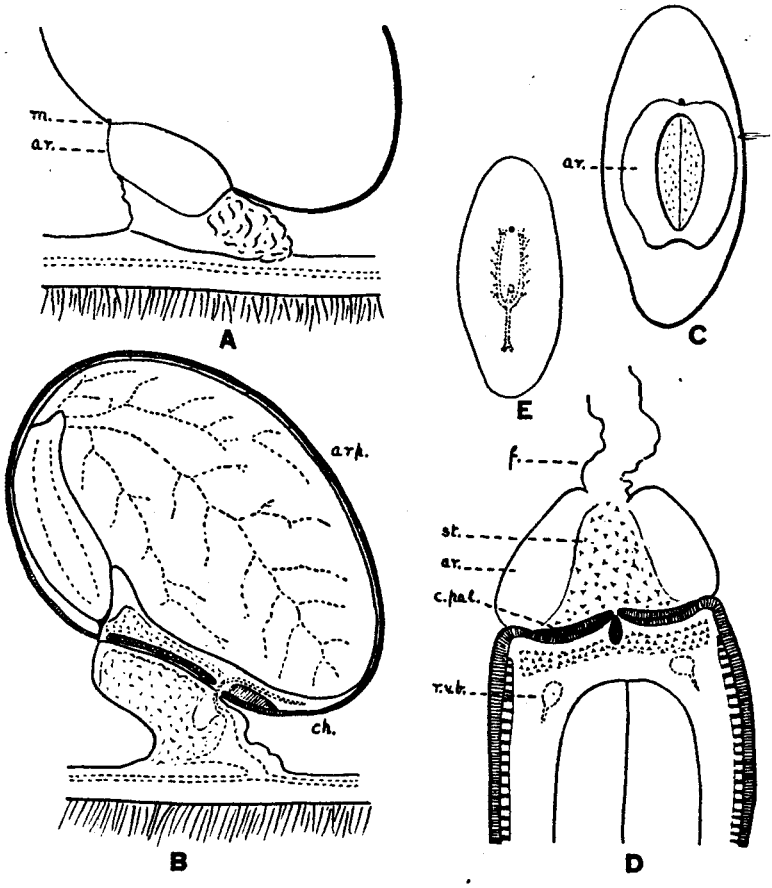

FIG. 18 — *Tephrosia candida* (Papilionaceae). A, lower part of the seed attached to the funicle, in surface view. B, seed in median longitudinal section. ×6. C, hilum in surface view with the funicle detached. ×6. D, hilum in transmedian longitudinal section. ×15. E, diagram of the vascular supply of the seed.

palisade-layers are practically confluent: hence, this palisade of the funicle-head, or *counter-palisade* of the hilum ('cellule de rinforzo' of Italian authors), adheres to the seed on separation from the funicle.

Both palisade and counter-palisade are interrupted along the mid-line by a very fine groove (the median or hilar groove), which can be seen in most Papilionaceous seeds with the naked eye, unless obscured by dried funicular tissue. The groove is an air-passage in the ripe seed. It develops as a break in the palisades in the same way as the pleurogram of Mimosoid seeds or by drying up of a small flange of parenchymatous tissue (as in the aril-lobes of *Bauhinia* and *Erythrina*, which I will describe in a later paper). The groove leads to the *tracheid bar* which, in the subhilum, is a rod of short tracheids extending the length of the hilum, from raphe almost to micropyle: at the raphe-

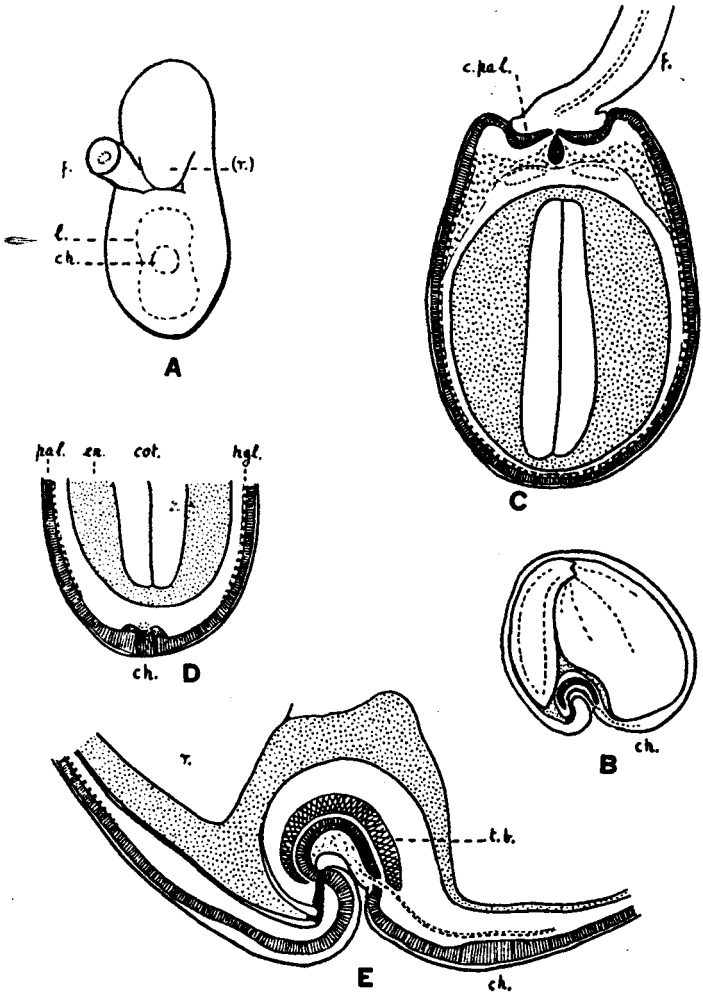

FIG. 19 — *Crotalaria retusa* (Papilionaceae). A, seed in hilar view (with the funicle attached). B, in median longitudinal section. ×6. C, D, E, sections of the seed, chalaza and hilum. ×15.

end it contacts the sheath of the v.b. or even the xylem, but it may also stop short of the v.b. In cross-section the tracheid bar is ovate and pointed to the hilar groove. The tracheids are contiguous, without parenchyma, and also point to the hilar groove: if short, they have reticulate pitting: if long, they are scalariform. The bar appears at an early stage in seed-development as a firm strand of watery tissue, surrounded by a narrow sheath of small-celled parenchyma. At maturity the thickened tracheids contain air, and the bar appears as a white strand in the subhilum. On either side of the bar is stellate aerenchyma, generally separated from the palisade by several rows of contiguous, thick-walled isodiam (etric cells as in the subhilum of Mimosoid and Caesalpinioid seeds). Beneath, or internal to, the tracheid bar and its aerenchyma is thin-walled parenchymatous tissue carrying the two recurrent v.b., which connect with the raphe v.b. at its entry to the seed: these v.b. do not extend beyond the hilum, though they may give off branches to the sides of the seed: following Pitot, I have called them the *recurrent vascular bundles*. The tracheid bar is the 'lamina chilariale' of Italian authors and the 'tracheid-insel' of Tschirch, so named from its appearance in cross-section.

Thus, the bean-hilum is a horny patch bordered by a vestigial aril, surfaced

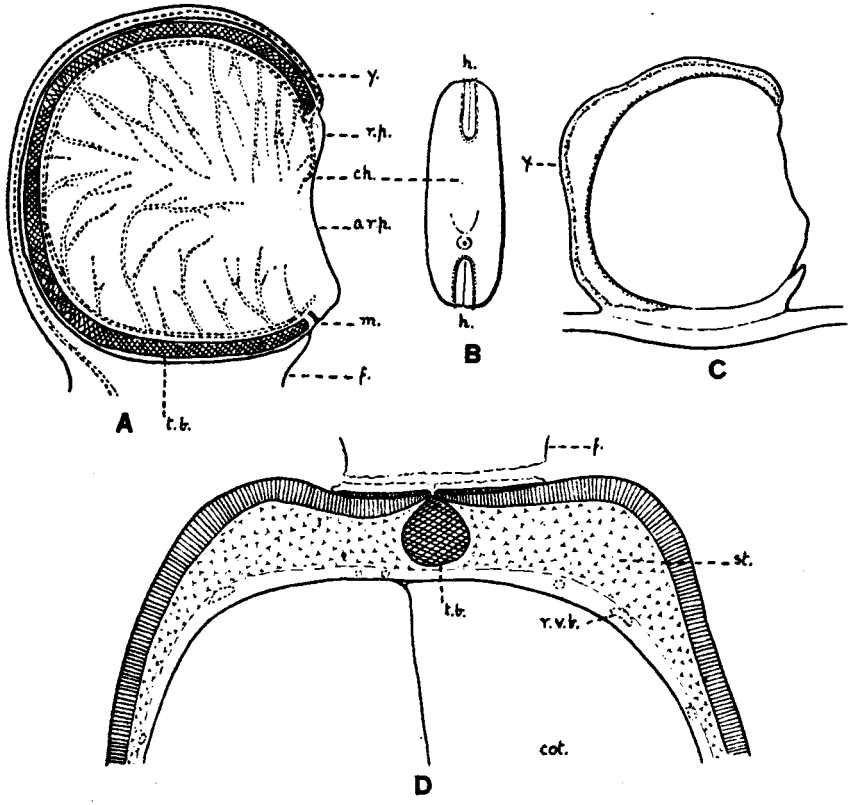

FIG. 20 — *Mucuna bennettii* (Papilionaceae). A, diagram of the seed to show the elongate hilum with long tracheid bar (hatched) and the vascular supply to one side of the seed from the recurrent v.b. B, C, seed in chalazal view and side-view (with the funicle-head, *y*, separating from the hilum). ×1½. D, transmedian longitudinal section of the hilum, with the funicle separating. ×15.

by the counter-palisade with median groove, supported by the tracheid bar, and carrying two vascular bundles. At the raphe-end there is often a horny lens, as in the Mimosoid-Caesalpinioid seed: at the other end are the micropyle and the slight eminence caused by the tip of the curved radicle.

VASCULAR SUPPLY — In contrast with the Mimosoid-Caesalpinioid seed, there is much variation in the vascular supply in the Papilionaceous. The variation

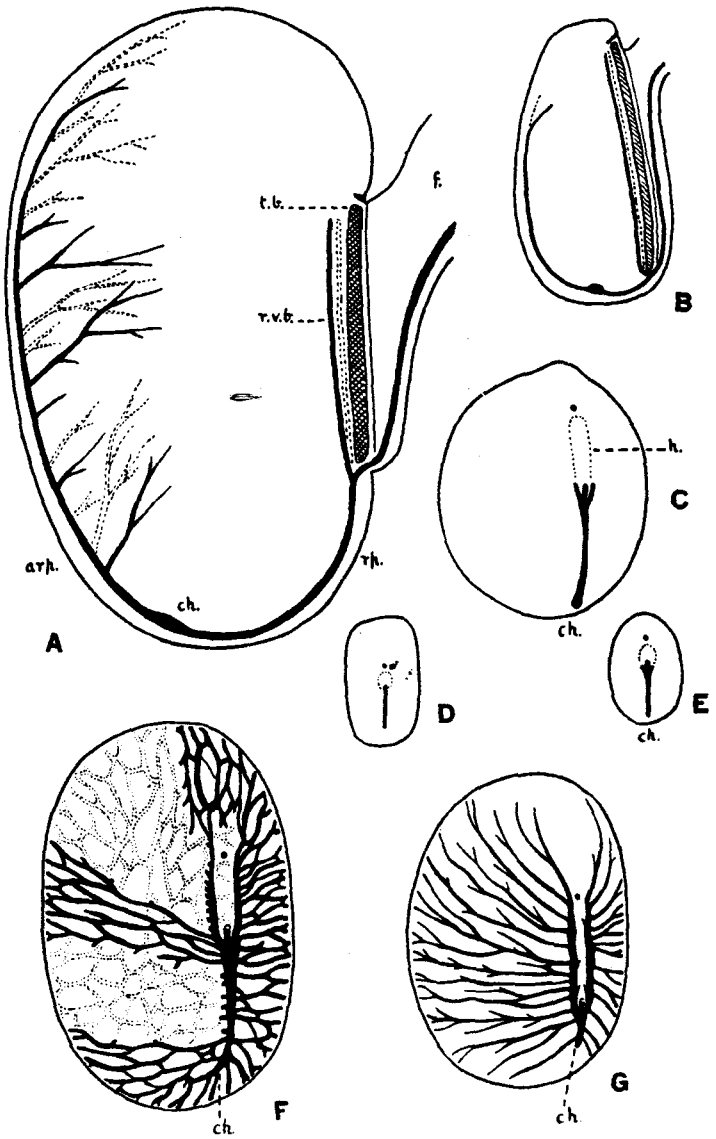

FIG. 21 — Diagrams of the vascular supply in Papilionaceous seeds (roughly to scale). A, *Canavalia ensiformis;* B, *C. mexicana;* C, *Sophora tomentosa;* D, *Indigofera enneaphylla;* E, *Abrus precatorius;* F, *Erythrina subumbrans* (a part only of the reticulum shown on one side of the seed); G, *Mucuna utilis* (with short raphe).

may well be systematic with generic, if not tribal, value. I will mention only the more extensive differences.

In *Canavalia ensiformis* (Fig. 21) there is a fairly long post-chalazal v.b. in the antiraphe, giving off short branches to the sides of the seed: the pre-chalazal v.b. is unbranched after giving off the two recurrent v.b. In *C. mexicana* (Fig. 21), which has an elongate hilum extending along the whole of one edge of the seed, the vascular supply is similar but the post-chalazal v.b. is short and merely forks into two branches ending about half-way to the micropyle.

In contrast are the seeds of *Mucuna* (Figs. 20, 21) and *Dolichos*, both of which have the elongate hilum. There is no post-chalazal v.b.: the pre-chalazal v.b. is very short (following the short raphe); but the recurrent v.b. are strongly developed along the length of the hilum and give off many branches to the sides of the seeds. *Vigna* is similar, but the hilum is shorter. (No Mimosoid or Caesalpinioid seed has this elongate hilum.)

In *Erythrina* (Fig. 21) there is an intermediate and more complicated state. Again, there is no post-chalazal v.b., but the pre-chalazal as well as the recurrent v.b. give off the branches to the sides of the seed, where they anastomose profusely, even re-forming into a false post-chalazal v.b. along the antiraphe.

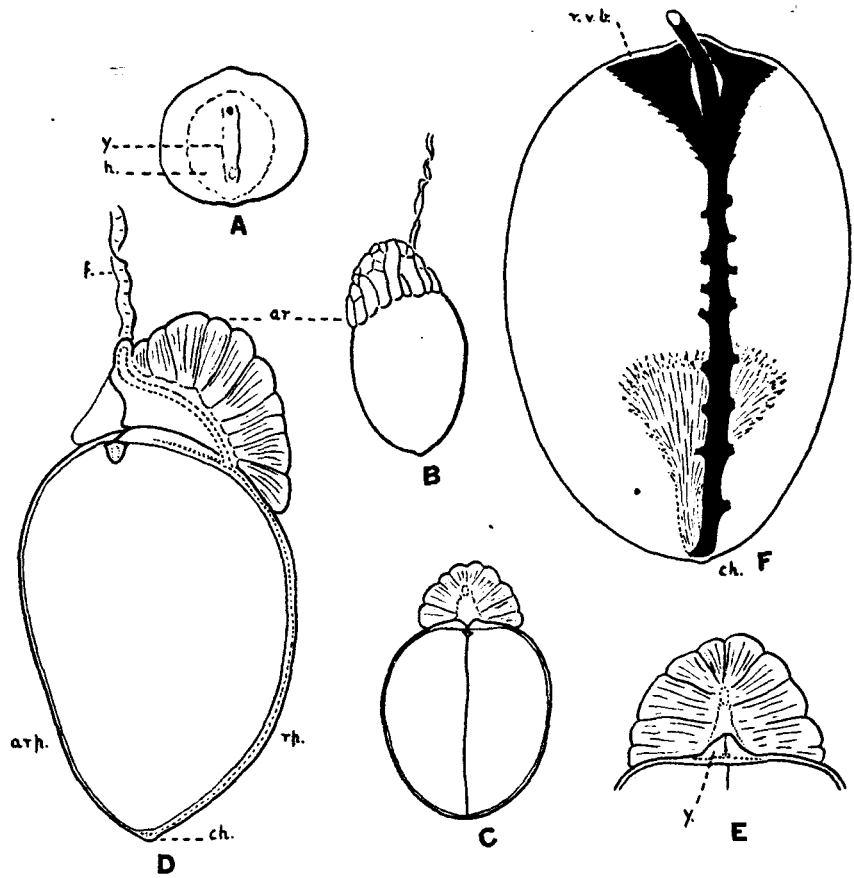

FIG. 22 — *Swartzia pinnata* (Swartzioideae). A, B, C, the seed in hilar view, side-view and t.s. ×1. D, E, the seed in median and transmedian longitudinal section. ×3. F, a diagram of the vascular supply of the seed. (*y*, bony ridge of hilum.)

In *Tephrosia*, *Sophora*, *Abrus*, and *Indigofera* (Fig. 21) there can be seen a progressive simplification in loss of branching (*Tephrosia*) and in shortening of the recurrent v.b. (*Sophora*, *Abrus*), until in the small seed of *Indigofera* there remains only the short v.b. of the raphe.

Thus, in the Phaseoleae for instance, there occur the vascular systems of *Canavalia*, *Mucuna*, *Erythrina*, *Phaseolus* (as in *Tephrosia*, or without recurrent v.b.) and *Rhynchosia*, which resembles *Abrus*. So the question may be raised whether this feature is not as important in classification as the construction of the flower. The vascular system of the seed indicates its manner of growth. In Canavalia there appears to be a general

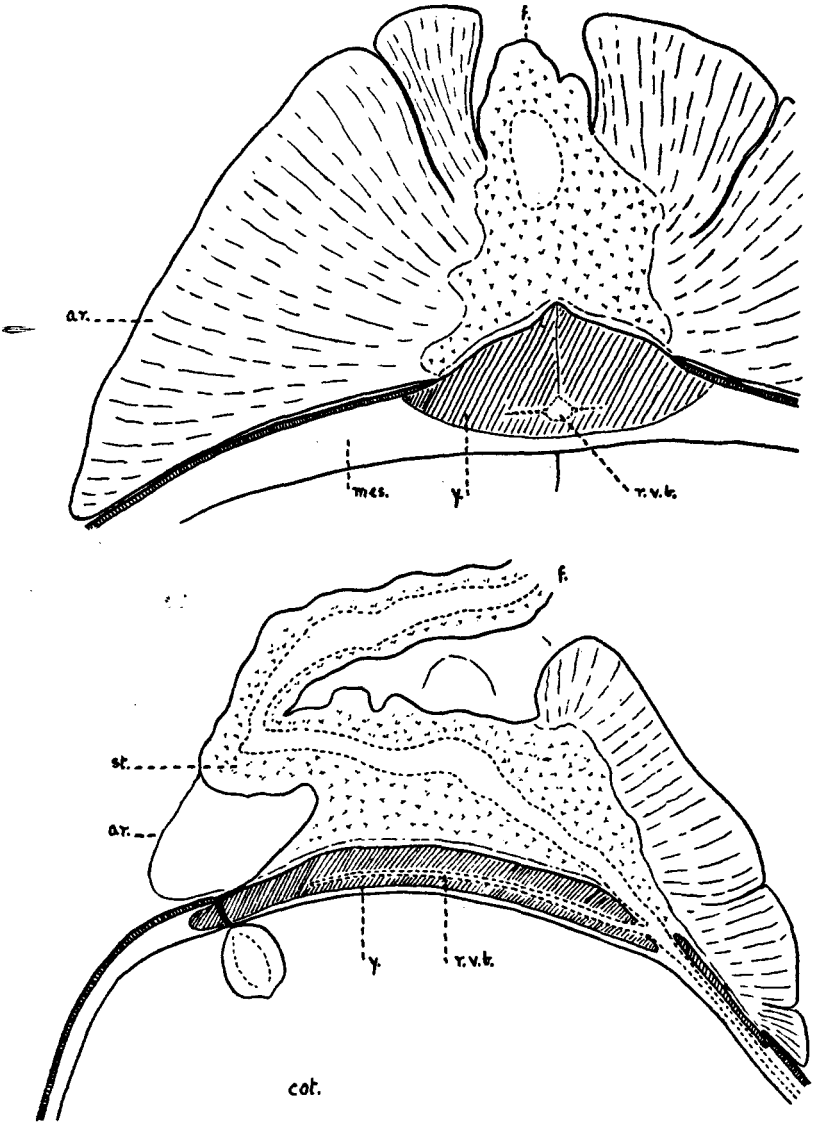

FIG. 23 — *Swartzia pinnata* (Swartzioideae). Median and transmedian longitudinal sections of the hilum. ×15. (*y*, bony ridge of hilum.)

enlargement of the ovule: in Mucuna the ovule elongates mainly in the hilar region: in Erythrina the antiraphe does not develop.

RADICLE — The rather long, curved radicle, typical of the bean seed, varies in some genera into the short median radicle of the Mimosoid-Caesalpinioid seed, as in *Sophora*. Short, straight, median radicles occur in the following genera:

Hedysareae: *Arachis*.

Galegeae: subtr. Brongniartieae (*Brongniartia, Harpalyce, Lamprolobium*): *Milletia* (pr. p.).

Viceae: *Cicer*.

Phaseoleae: *Voandzeia*.

Dalbergieae: *Andira, Dipteryx, Euchresta, Fissicalyx, Geoffraea, Pterodon*.

Sophoreae: *Alexa, Bowdichia, Bowringia, Camoensia, Castanospermum, Dalhousiea, Diplotropis, Monopteryx, Myrocarpus, Ormosia, Sophora* spp., *Sweetia* spp.

Though the character appears to be the unspecialized condition associated with the symmetrical seed, it may also be a consequence of overgrowth of the seed and resultant lack of orientation of the embryo (*vide infra*).

The Seed of *Swartzia pinnata*

The seed of this tropical American tree offers the only intermediate state, that I have encountered, between the Mimosoid-Caesalpinioid construction and the Papilionaceous. In floral construction, too, the Swartzioideae appear intermediate between the Caesalpinioideae and the Sophoreae. It is to be hoped that seeds of other species of *Swartzia* and of related genera can soon be examined: those of *Aldina*, with massive and radially symmetrical flowers, seem unfortunately to be overgrown and unlikely to be helpful (*vide infra*).

The seed of *S. pinnata* has the following Mimosoid-Caesalpinioid characters:

Long funicle, large aril, symmetrical shape with equal raphe and antiraphe, no extensive v.b. on the sides of the seed, no

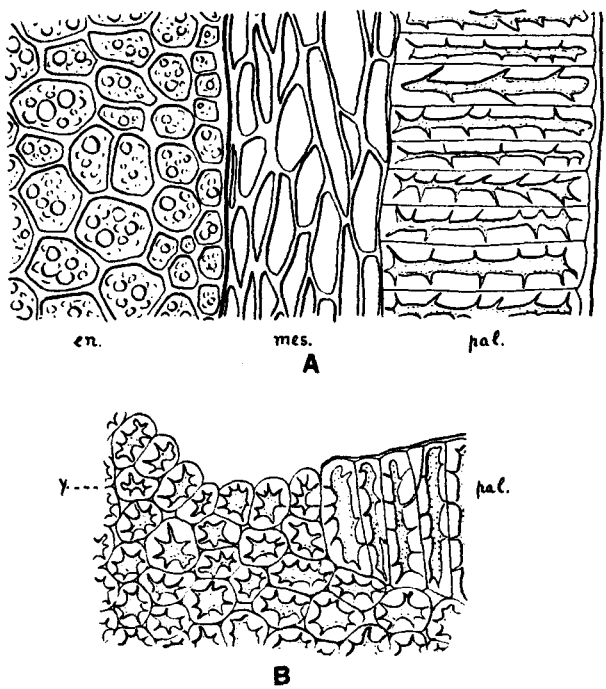

FIG. 24 — *Swartzia pinnata* (Swartzioideae). Transverse sections of the testa, on the side of the seed A, and at the junction with the bony ridge, *y*, of the hilum, B. ×350.

counter-palisade, and a short, straight radicle.

But it has three Papilionaceous features, at least incipient : a shortening of the post-chalazal v.b., the presence of a recurrent v.b. in the subhilum, and a bony ridge along the hilum suggestive of the tracheid bar.

Its own peculiarities are the absence of hilar palisades, the bony ridge of the hilum, and the union of the two recurrent v.b. into one band of vascular tissue, which comes to lie in the bony ridge after the ground-tissue of the subhilum has become thick-walled.

Thus the seed appears mainly Mimosoid-Caesalpinioid, but it has incipient the features of the bean-hilum. Refinement of the diffuse and large hilum of *S. pinnata* could lead to that of the bean (for detailed description, see the account at the end of this paper).

Overgrown Seeds

The Leguminous seed has normally a specific size set by differentiation of the palisade at a certain stage of development of the fruit and seed. As a result the pod conforms with the seeds. In some cases, in contrast, the seed enlarges and fills the seed-cavity of the pod without differentiation of the features of the Leguminous testa. Such seeds, conforming with the pod, are exalbuminous and have the nature of tumours, the growth of which is limited by the size of the pod : hence I refer to them as *overgrown seeds*. Their main character is the lack of differentiation of the testa, which remains embryonic.

Overgrown seeds occur in the following genera:

Mimosoideae : *Entada*, *Pentaclethra*, *Pithecellobium* pr. p. (e.g. *P. jiringa*).

Caesalpinioideae: (*Amherstia* ?), *Bauhinia* pr. p., *Brownea*, *Cynometra*, *Detarium*, *Dialium*, *Koompassia*, *Mora*, *Saraca*.

Swartzioideae: *Aldina*.

Papilionatae: *Andira*, *Arachis*, *Castanospermum*, *Inocarpus*, *Millettia* pr. p., and probably most genera or species with large, thin-walled seeds in indehiscent fruits (e.g. *Dalbergia*, *Derris*, *Dipteryx*).

Millettia atropurpurea (Papilion., Galegeae; Figs. 25, 26) — The large leathery pods contain 1-4, mostly 2-3, large seeds on short funicles, and they are very tardily dehiscent.

The testa (Fig. 26) consists of more or less superposed rows of stellate cells, the walls of which become irregularly thickened with re-entrant processes on the ripening of the seed. The outer integument thickens in development by periclinal and anticlinal divisions of the epidermal cells: no differentiation occurs and, on ripening, the cells are merely dried off in various stages of growth. Similarly there is no differentiation in the hilum which lacks rim-aril, median groove, palisades, tracheid bar, and recurrent v.b. The vascular supply consists of a pre-chalazal v.b. spreading into 3-4 strands in its course, and of 5-6 v.b. divergent from the chalaza over the sides of the seed, but without a true post-chalazal v.b. Two very short processes from the v.b. of the raphe may be traces of the recurrent v.b.

Thus, this seed is an enormous embryonic growth with minimum differentiation, filling the cavity of the legume. Its embryo has lost its orientation, but the thinness of the testa allows the radicle to burst through anywhere. The only Papilionaceous marks are the slightly shorter raphe (compared with the antiraphe) and the absence of the post-chalazal v.b.

In the following table I have given a few measurements that I made on some pods with their seeds:

Millettia atropurpurea — Fresh weight (gms.) of fallen pods and their contained seeds.

Seeds per pod	Av. wt. of seed	Total av. wt. of seed per pod	Av. wt. of empty pod	Total av. wt. of pod & seed	Range of seed-wt.	No. of seeds weighed
1	61·8	61·8	29·1	90·9	57·4-67·1	4
2	65·4	130·8	54·8	185·6	55·2-72·0	8
3	47·6	142·8	54·2	197·0	34·0-58·9	12

seeds. The mature testa consists of undifferentiated parenchyma with th· cells somewhat radially elongate and with slightly thickened brownish walls. As in all Amherstieae (and Cynometreae) that I have studied, the hilum has no palisade. The v.b. of the raphe-antiraphe is dilated into a broad band giving off very short processes which barely reach the sides of the seed. In *Brownea* (Amherstieae), the construction is similar but the laterals of the v.b. anastomose over the sides of the seed as in *Pentaclethra*.

Bauhinia (Caesalp. ; Fig. 27) — In this large genus every transition seems to occur from normally constructed seeds of medium size to fairly large, overgrown seeds with undifferentiated testa, but without elaboration of the vascular supply. Thus, *B. variegata* and *B. fassoglensis* have a well-developed palisade with *linea lucida*: in *B. picta*, the palisade-cells are not so well-formed and lack the *linea lucida*: in *B. purpurea*, the palisade-cells are very short: in *B. flammifera*, they are scarcely differentiated.

The largest overgrown Leguminous seeds appear to be the flattened seeds of *Mora excelsa* (Caesalp., Dimorphandreae), 12·5 × 7 cm. (? thickness) with membranous testa (those of *Dimorphandra* seem to resemble those of *Erythrophloeum*, but lack the strong mucilage-stratum of the palisade). The seeds of *Aldina* (Swartzioideae) and *Andira* (Sophoreae) may be as massive, but are rounded.

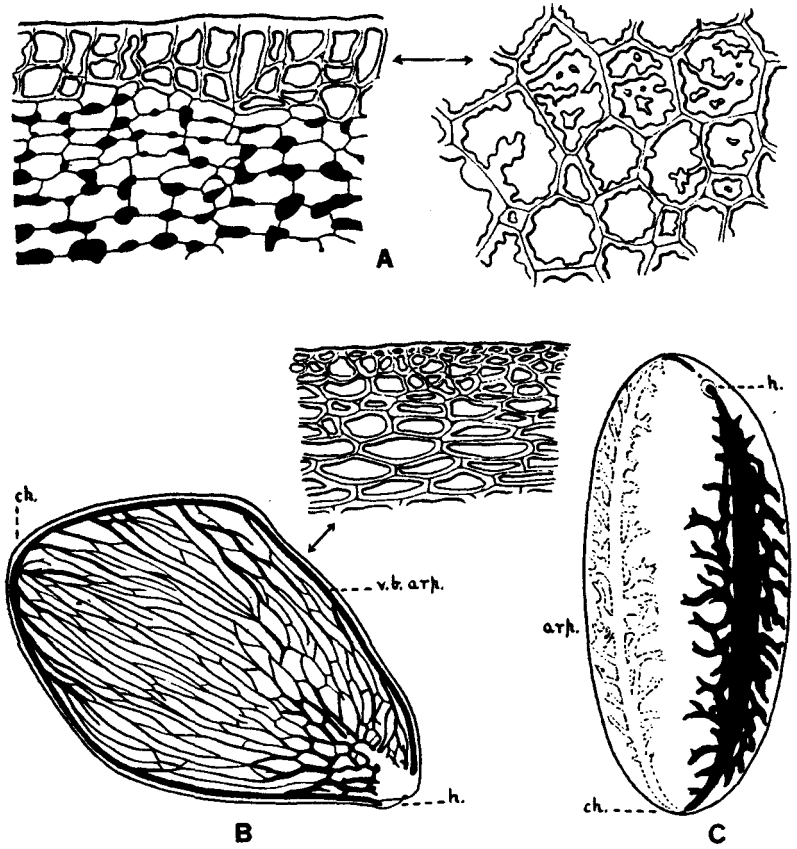

FIG. 26 — Overgrown seeds. A, *Millettia atropurpurea* (Papilionaceae), the testa in section, ×225, and surface view, ×350. B, *Pentaclethra filamentosa* (Caesalp.), a diagram of the vascular supply of the seed, ×1½, and the testa in t.s. ×225. C, *Saraca declinata* (Caesalp.), a diagram of the vascular supply of the seed. ×1½.

Aeration, Water-supply and Mechanical Construction

After fertilization the ovary develops rapidly into the immature photosynthetic legume. Less quickly the ovule becomes the full-sized, but immature, photosynthetic seed, and lastly the embryo slowly becomes chlorophyllous and full-grown, but, as it rarely forms starch, its early photosynthetic activity may be incomplete. At length, legume, seed-coat and embryo dry off in the same order, the embryo losing its green colour. The only non-chlorophyllous part of the seed is the endosperm. The fruit-wall and seed-coat must contribute in some measure photosynthetically to the requirements of the embryo. (In the Cucurbitaceous seed-coat a woody layer soon develops beneath the outer photosynthetic layer, which is then cut off from the embryo and, on drying off of the seed, its dead cells are full of useless starch.)

Aeration of the seed, as judged from the occurrence of aerenchymatous tissue, must proceed through the subhilar tissue, either by way of the funicle or by way of the endocarp cavity, and thence between the hour-glass layers. The epidermis of the young seed, on developing the palisade, must soon become more or less impervious to gaseous exchange. The enlargement of the hilum and the shortening of the funicle in the Papilionatae thus appear as means of facilitating aeration and, so, the growth of the seed.

The meagre vascular supply of the Mimosoid-Caesalpinioid seed appears to be improved upon by the tracheid bar, as a water-reserve, in the Papilionatae. It is well known that, in detached shoots, the transpiring leaves withdraw water from the immature fruits, which become wilted in consequence with adverse effects on the embryo. In this light the tracheid bar, as a reserve for maintaining the turgidity of the embryo, must increase the efficiency seed. The endocarp-pith, or 'früchtbrei', of the legume may have a similar function where well-developed, as in *Cassia*, *Hymenaea* and *Parkia*, by supplying water directly through the immature palisade of the seed.

The obvious mechanical and protective part of the Leguminous seed is the pali-

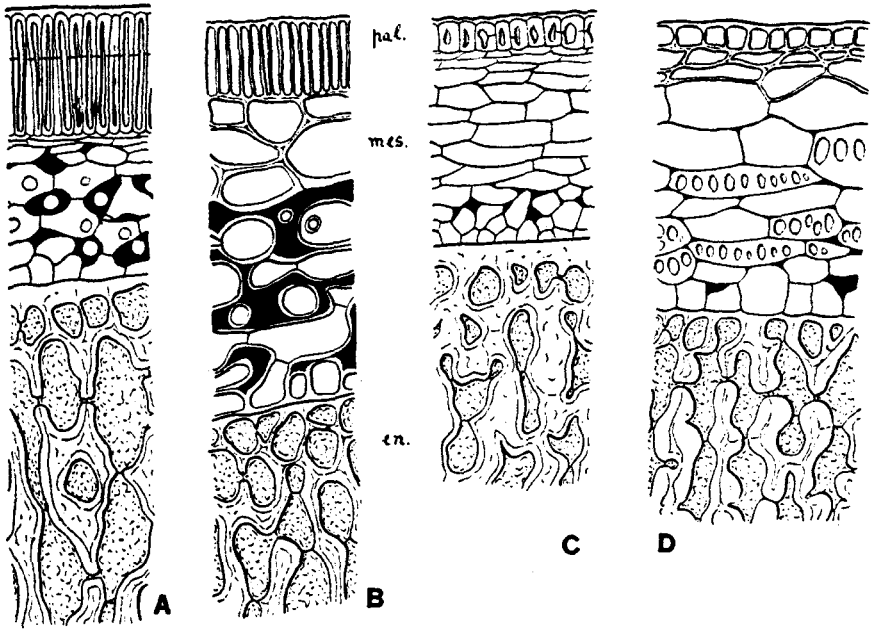

FIG. 27 — Transverse sections of the testa in *Bauhinia* (Caesalp.). A, *B. variegata*; B, *B. picta*; C, *B. purpurea*; D, *B. flammifera*. ×225.

sade: to a less extent, the mesophyll, when thick-walled, will act as a cushion between the palisade and the embryo. It seems that there is necessity for protection of the embryo against the strong compression induced by the drying and shrinking of the testa. The thick-walled tissue of the raphe-antiraphe, and of the subhilum, as well as the tracheid bar, must act as struts withholding the effect of this compression from the edges of the cotyledons and the tip of the radicle.

The dried out hilum, by way of its median groove in the Papilionatae, and the dried out tracheid bar may again serve for aeration of the germinating seed.

In contrast, the overgrown seed provides better aeration, by lack of differentiation of the palisade (even with stomata in *Inocarpus*), better vascular supply by ramification of the bundles over the sides of the seed, and less need for mechanical protection in the thin testa. But such seeds, other things being equal, will have less power to withstand desiccation and will be limited environmentally to humid forests or humid soil (*Arachis*).

The intricate structure of the seed presents morphological and physiological problems, revealing the Papilionaceous seed as the most elaborate and, if one may judge from rapidity in growth, the most efficient.

Conclusions

My conclusions on the structure of the Leguminous seed can be summarized most conveniently in the following key:

Key to Leguminous Seeds

Hilum with rim-aril, counter-palisade, median groove, and, typically, two recurrent v.b., mostly exalbuminous, with short funicle, curved radicle, and thin-walled cotyledon-cells: raphe shorter than the antiraphe: no pleurogram ... ... Papilonatae

Hilum without such features: radical typically short, straight, median: funicle often long: often albuminous: raphe equal to or longer than the antiraphe

Hilum elongate with superficial bony ridge of isodiametric, sclerotic cells and with a single broad recurrent v.b.: seed symmetrical: cotyledon-cells thick-walled, with starch ... Swartzia

Hilum not so, generally small and closed by a palisade

Hilum more or less crescentic through the presence of one or two aril-lobes: raphe usually longer than the antiraphe and then without post-chalazal v.b.: hour-glass cells absent: lens micropylar: cotyledon-cells thin-walled ... ... Bauhinia

Hilum round or shortly oblong, generally small: raphe equal to the antiraphe: post-chalazal v.b. present: lens on the raphe

Hilum minute, linear-oblong or ovoid, without palisade: funicle short or swollen by the arillode: cotyledon-cells thick-walled ... ... Amherstieae, Cynometreae

Hilum subcircular, small, closed by the palisade: funicle often long: cotyledon-cells thin-walled

Pleurogram present

Pleurogram as a fine groove open toward the hilum: mostly exalbuminous ... Mimosoideae

Pleurogram complete, without groove: albuminous ... ... Cassia

Pleurogram absent ... ... Caesalpinioideae et Mimosoideae ceterae

smaller than Leguminous (except in some Chrysobalanoideae): indeed, the least differentiation of the Rosaceous testa occurs in the smallest Rosaceous seeds, in strong contrast with the Papilionatae. Thus, the Rosaceous seed is not only differently constructed from the Leguminous, but evolves in a different way. Its structure agrees with that of many other Dicotyledonous families, whereas the Leguminous structure stands by itself. Floristically and, perhaps, vegetatively, there is no Rosaceous plant more primitive than *Archidendron* of the Mimosoideae. Hence I conclude that there are no grounds for the disruption of Leguminosae or for inferring any close affinity between the Mimosoideae and the Rosaceae.

Summary

An attempt is made to show the systematic importance of the structure of the Leguminous seed. The family is characterized by the outer epidermal palisade of the outer integument and its hypodermal layer of hour-glass cells. The cell- and tissue-layers of the testa are described in detail. The Papilionaceous seed is characterized particularly by the hilum which has, typically, a rim-aril, median groove, counter-palisade, tracheid bar, and two recurrent vascular bundles. The seed of *Swartzia pinnata* suggests that the Swartzioideae may have a seed-structure intermediate between that of the Papilionaceous and the Mimosoid-Caesalpinioid. The *Bauhinia*-seed is a counterpart of the Papilionaceous, rather than an ancestral condition. The Mimosoid seed is indistinguishable from the Caesalpinioid except for the presence, in many genera, of a roughly heart-shaped groove on the sides of the seed, called the *pleurogram*. The vascular supply of the Papilionaceous seed may have generic, if not tribal, value

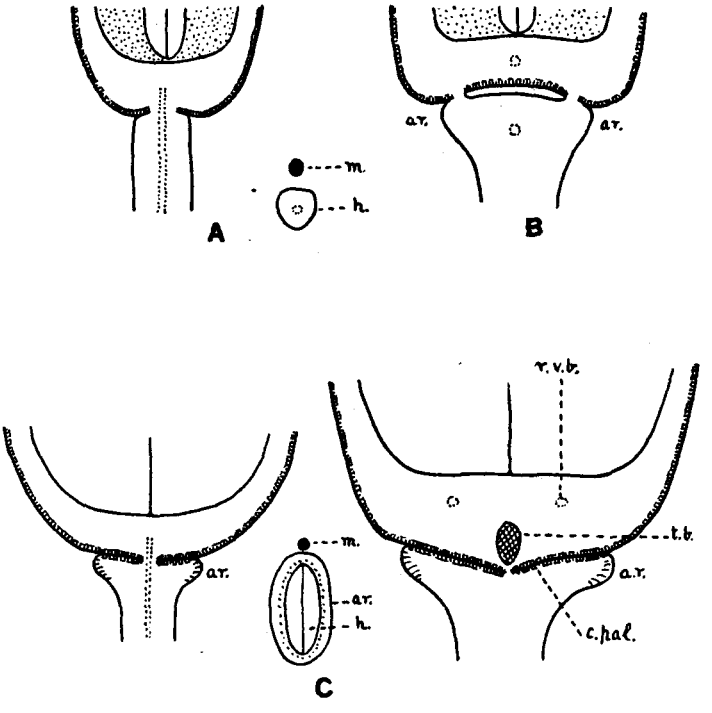

FIG. 29 — Diagrams of hilum of Leguminous seeds in transmedian longitudinal section. A, Mimosoid-Caesalpinioid seed, with surface view of hilum and micropyle. B, Bauhinia modification. C, Papilionaceous seed, with the hilum in surface view.

in classification. In all four subfamilies there occur large seeds with undifferentiated testa, and such are called *overgrown seeds*. The Rosaceous seed has none of the characteristics of the Leguminous, and it is concluded that alliance of the Mimosoideae with the Rosaceae is unjustified.

Description of the Seeds Figured

MIMOSOIDEAE — *Adenanthera pavonina:* seeds 8-9 × 5 mm., scarlet, shiny, subcordate, with pleurogram: *hilum* 0·6 mm. wide, elliptic, closed by the palisade: *funicle* 3-5 mm. long, pink, with slight aril (covering the micropyle): *endosperm* horny, thick walled.

Testa thick, very hard: *palisade* with long cells, the walls thickened and orange red, swelling strongly in water and the colour dissolving, without linea lucida, but with slight mucilage-stratum (except at the beginning of the raphe): *hour-glass cells* absent: mesophyll of thick-walled, colourless cells, contiguous near the palisade, substellate toward the *i.i.*, with a slight indication of an inner layer of hour-glass cells: *pleurogram* without modification of the testa: *lens* absent: *v.b.* simple, without flexure: *cotyledon-cells* with slightly thickened walls and few minute (1-2μ) starch-grains or none.

Albizzia sp. (aff. *A. odoratissima*): seed 10 × 7·5 × 2·5 mm., ellipsoid, flattened, straw-colour, with semi-elliptic pleurogram: *hilum* c. 0·8 mm. wide, round, closed by the palisade: *funicle* 10-12 mm. long, exarillate: *endosperm* slight, thin-walled.

Testa thin, hard: *palisade* rather short, without mucilage-stratum, with linea lucida: *hour-glass cells* as a single outer layer, short, absent from the raphe-antiraphe: *mesophyll* with thick-walled contiguous cells, substellate in the subhilum: *pleurogram* with the testa modified by thickening of the palisade (particularly the outer layer), with 3-4 rows of *hour-glass cells* (often ill-defined), and with thickening of the mesophyll (indenting the cotyledon): *lens* small: *v.b.* simple, passing internally to the lens, with marked flexure: *cotyledon-cells* thin-walled, oily, with few, small, starch-grains.

Mimosa pudica: seed 3·5 × 3 × 2 mm., pale brown, flattened-ovoid, with pleurogram: *hilum* 0·05 mm. wide, circular, closed by the palisade: *funicle* 1·5-2 mm. long, coiled once: exarillate: *endosperm* abundant, horny, thick-walled.

Testa thin, hard: *palisade* with linea lucida, no mucilage-stratum: *hour-glass cells* as a single short row, absent from the raphe-antiraphe: *mesophyll* with thick-walled, contiguous cells, stellate in the subhilum: *pleurogram* with slightly enlarged *hour-glass cells: lens* ill-defined, at the beginning of the raphe: *v.b.* single, passing through the lens with slight flexure: *cotyledon-cells* thin-walled, oily, without starch.

Parkia javanica: seeds 25 × 12 × 10 mm., dull black, with large pleurogram: *hilum* 0·3 mm. wide, very small, subcircular, closed by the palisade: micropyle subcrenulate: *funicle* 15-20 × 0·25 mm., coiled: exarillate: exalbuminous.

Testa thick, hard: *palisade* well-developed, with mucilage-stratum (absent or slight round the hilum) and linea lucida, the inner layer of the palisade-cells having brownish walls: *hour-glass cells* present only immediately below the pleurogram and there often ill-defined: *mesophyll* thick-walled, substellate, the walls and lumen of the cells brownish, stellate in the subhilum: *pleurogram* with shorter palisade (with reduced mucilage-stratum) and ill-defined hour-glass cells: *lens* absent: *v.b.* simple, slender, without flexure : *cotyledon-cells* thin-walled or the walls slightly thickened at the angles, without starch: no oil-glands.

Pentaclethra filamentosa: seed 40-50 × 25-30 × 7-9 mm., dull brown, without pleurogram, flattened and trapeziform, overgrown: *hilum* 2·5 mm. long, oblong: *funicle* 1·5-2 mm. long, short, flattened-conical: exarillate: exalbuminous.

Testa thinly leathery, composed of undifferentiated, somewhat thick-walled, cells: palisade, *hour-glass cells* and stellate cells absent: *v.b.* branching along the whole course of the raphe-antiraphe, the branches anastomosing on the sides of the seed and converging to the hilum: *cotyledon-cells* thin-walled, oily, without starch; oil-glands abundant in the cotyledonary tissue.

CAESALPINIOIDEAE — *Bauhinia picta:* seed 16 × 10 × 3 mm., compressed bean-shaped, with asymmetric, slightly prominent chalaza, brownish-ochre: *hilum* 0·4 mm. wide, circular with two, equal lines (c. 4 mm. long) curving along the raphe (the line of aril-attachment), covered by the palisade: *funicle* 4 mm. long, short, thick, curved under the seed, with two short ridge-like aril-lobes detaching from the mature seed: *endosperm* horny, without starch, abundant.

Testa tough: *palisade* short, the cell-walls scarcely thickened, without linea lucida (except in the hilum-palisade) or mucilage-stratum: *hour-glass cells* absent: *mesophyll* parenchymatous with slight thickened walls, substellate in the inner part, stellate in the subhilar tissue: *lens* surrounding the micropyle: *v.b.* simple, without post-chalazal extension: *cotyledon-cells* thin-walled, without starch.

B. purpurea, B. rosea and *B. violacea*: as in *B. picta* but:— without conspicuous chalaza: *aril-lobe* single, short (1·5 mm. long): *endosperm* reduced to a microscopic film: *palisade-cells* scarcely elongate, without linea lucida: *mesophyll* undifferentiated: *v.b.* with a short recurrent process in the subhilum.

B. variegata: as in *B. picta* but palisade-cells longer, with the linea lucida present throughout:

mesophyll mostly substellate, with slightly thickened walls.

B. fassoglensis: seed 25×22×4 mm. (uncontracted), brown, ovoid-compressed, nearly symmetrical, the antiraphe little shorter than the raphe: *hilum* as in *B. picta: funicle* 10 mm. long, broad, flattened: aril-lobes 2, 5-6 mm. long: exalbuminous, or with a very thin residual film of endosperm.

Testa rather thick, firm: *palisade* well-formed, the thick-walled cells with diffluent anticlinal walls and conspicuous linea lucida: *hour-glass cells* absent: *mesophyll* composed of narrow outer and inner layers of small-celled parenchyma with an intermediate, wide layer of substellate cells: subhilar tissue stellate: *lens* well-formed round the micropyle, the palisade thin over the lens: *v.b.* simple, extending along the raphe-antiraphe and with a short recurrent process in the subhilum.

B. flammifera: seed 25×20×4-5 mm., ovoid-compressed, brown: *funicle* 12×4-5×0·5 mm., flattened: *aril-lobes* absent: *endosperm* copious, horny.

Testa thin: *palisade-cells* isodiametric, slightly thick-walled, scarcely differentiated: *mesophyll* parenchymatous, not stellate, becoming slightly thick-walled and shallowly pitted: *v.b.* simple, with a short recurrent process in the subhilum, without post-chalazal extension: *cotyledon-cells* thin-walled.

Delonix regia: seed 17-25×5 mm., oblong, subfusiform and subcompressed, often slightly 4-angled in t.s., fuscous brown with four pallid bands (vaguely delimited) along the angles from the hilum: *hilum* 0·8 mm. wide, round, closed by the palisade: *funicle* 7-8 mm. long, bent at the apex: exarillate: *endosperm* abundant, grey, horny, thick-walled.

Testa thick, hard: *palisade* with linea lucida, no mucilage-stratum, invaginated round the *v.b.* at the raphe: *hour-glass cells* in two short outer rows and a single short inner row, with dark brown contents, absent from the raphe-antiraphe and from the four pallid bands on the angles of the seed: *mesophyll* of thick-walled, contiguous cells with brownish contents, stellate-columnar in 6-7 rows beneath the four pale bands, stellate with long arms in the subhilum: *lens* present at the beginning of the raphe and surrounding that side of the hilum: *v.b.* simple, passing through the invaginated palisade-tube, then passing to the inner side of the lens with a strong flexure: *cotyledon-cells* thin-walled, oily, with few, minute, starch-grains.

Erythrophloeum guineense: seed 20×15×7 mm., elliptic-quadrate, subcompressed, with bright green contents and thick gelatinous outer layer (except for the depressed band of the raphe-antiraphe), then drying dark grey-brown and cracked: *hilum* 0·6 mm. wide, ellipsoid, closed by the palisade: *funicle* c. 16 mm. long, flattened and strap-shaped, folded at the apex, greenish yellow: exarillate: *endosperm* abundant, horny, oily, non-amyloid.

Testa thickly gelatinous when moist, drying cracked: *palisade* with well-developed mucilage-stratum (much reduced on the raphe-antiraphe), linea lucida absent (except from the hilum-palisade, which lacks the mucilage-stratum), the cell-lumina with yellow oily matter: *hour-glass cells* well-developed as a single outer row all over the seed except at the hilum, no inner layer: *mesophyll* of thick-walled, sparsely pitted, contiguous cells, stellate in the subhilum: *lens* absent: *v.b.* without flexure: *cotyledon-cells* thin-walled, oily, without starch.

(*E. succirubrum* similar but the mucilage-stratum short all over the seed and, thus, the seed without the depressed median longitudinal band.)

Saraca declinata: seed 40-45×30-35×13-15 mm., elliptic-compressed, greyish brown: *hilum* 1 mm. wide, ellipsoid, without palisade: *funicle* very short, thick: exarillate: exalbuminous.

Testa thin, undifferentiated, without palisade, *hour-glass cells* or stellate tissue: *v.b.* somewhat flattened and ribbon-like, giving off short, irregular processes along its whole length (except at the chalaza), the processes scarcely extending on to the sides of the seed: *cotyledon-cells* with semicircular, non-amyloid, thickenings on the walls, with many small starch-grains.

SWARTZIOIDEAE — *Swartzia pinnata:* seed 25-30×20 mm., plump. heart-shaped, symmetrical, not compressed, yellowish fuscous mottled black, shiny: *aril* thick, crisp, juicy, white, as a compressed, lobulate, conical mass round the head of the funicle and obscuring the hilum, tasting sweetish, then bitter: *funicle* 15-21 mm. long, twisted, dangling, tough, white: exalbuminous: *hilum* (hidden by the aril) as a depressed area round a pale brown, hard, bony ridge slightly bifurcate at the micropyle.

Testa thin, easily drying and cracking, then peeling off (the seeds soon killed by desiccation): *palisade* columnar, the anticlinal walls obliquely pitted, without mucilage-stratum or linea lucida: *hour-glass cells* absent: *mesophyll* parenchymatous, slightly thick-walled at maturity, substellate in the subhilum: *bony ridge* of hilum composed of very thick-walled, pitted, isodiametric cells, more or less contiguous, with a rather abrupt transition to the palisade: *head of the funicle* with a layer of small isodiametric, thick-walled cells abutting on to the bony ridge (as an incipient counter-palisade): *lens* absent: *v.b.* flattened in the pre-chalazal part and giving off very short processes to the sides of the seed, and in the subhilum giving off two recurrent *v.b.* uniting on passing along the tissue of the bony ridge to the micropyle, the post-chalazal v.b. rather short, unbranched but expanding into a fan at the end: *cotyledon-cells* with the walls strongly thickened at the angles (non-amyloid), with abundant large starch-grains.

PAPILIONACEAE — *Crotalaria retusa:* seed 6×4×2·5 mm., reniform, compressed, light brown, very smooth, even slippery, separating from the funicle before dehiscence of the pod: *hilum* small, concealed in the curvature of the seed, with microscopic rim-aril: *funicle* c. 2×0·5 mm., relatively long, cylindric, the dried dead head remaining in the hilum: *endosperm* copious, horny, thick-walled.

Testa thin: *palisade* rather short, with distinct mucilage-stratum, particularly round the hilum, but scarcely evident at the chalaza, without linea lucida, cell-contents pale yellowish brown, the palisade-cells markedly elongate at the chalaza with their inner ends projecting into the substellate tissue of the mesophyll: *hour-glass cells* in a single, well-developed row, absent from the chalaza and the vicinity of the hilum: *mesophyll* with a single outer row of substellate cells and a few rows of thin-walled parenchymatous cells, stellate-celled in the subhilum: *lens* well-formed, extending from the hilum along the short raphe and surrounding the chalaza, composed of contiguous, thick-walled cells: *vascular supply* consisting of the short pre-chalazal v.b. and two short, scarcely differentiated, recurrent v.b., without branches to the sides of the seed: *counter-palisade* well-developed: *cotyledon-cells* thin-walled, oily, without starch.

Mucuna Bennettii: seed c. 20×20×10 mm., subcircular in outline, compressed, black, very hard: *hilum* extending round the greater part of the seed, with a very slight rim-aril: *funicle* short, the head extended round the hilum and separating as a hoop from the ripe seed: exalbuminous.

Testa very hard, thick, as in *M. utilis* and with similar vascular supply: *cotyledon-cells* with slightly thickened angles to the walls, swelling strongly in water and extruding the starch-grains with the other cell-contents.

Mucuna utilis: seed 26×16×11 mm., bean-shaped, compressed but rather plump, greyish white or slightly mottled: *hilum* 7×1 mm., oblong, surrounded by the horny, slightly crenulate, pale olive yellow aril c. 1 mm. thick: *funicle* short, broad, thick, but flattened: exalbuminous.

Testa leathery: *palisade* well-formed but without linea lucida (except in the hilum) and mucilage-stratum: *hour-glass cells* in a single row, well-formed, absent from the raphe: *mesophyll* consisting of a thin outer layer of substellate cells, 1-2 rows thick, a middle fairly thick parenchymatous layer, and an inner layer of very narrow, thick-walled, stellate cells with intricate arms, with a thick layer of stellate-celled tissue in the subhilum: *tracheid bar* composed of reticulately pitted tracheids: *lens* well-developed: *vascular supply* with short pre-chalazal v.b. and well-developed recurrent v.b. giving off branches to the sides of the seed, the branches dividing, but rarely anastomosing, without post-chalazal v.b.: *funicle* with rather poorly developed counter-palisade: *cotyledon-cells* slightly thick-walled, with large starch-grains.

Tephrosia candida: seed 8×5×3 mm., compressed-ovoid, fuscous black: *hilum* 2×0·8 mm., ellipsoid, with a relatively large, collar-like, whitish or pale yellow, horny rim-aril: *funicle* short, broad, compressed, horny on the raphe-side: exalbuminous.

Testa rather thick and firm: *palisade* well-formed, without linea lucida and mucilage-stratum: *hour-glass cells* in a single row, longer round the hilum, shorter towards the other side of the seed: *mesophyll* parenchymatous, with many swollen, rounded, cells containing white latex (as in the pericarp), the innermost layer consisting of substellate cells: *subhilum* with several layers of thick-walled cells next the palisade and a broad zone of substellate aerenchyma: *lens* well-developed: *vascular supply* consisting of the short pre-chalazal v.b. and two recurrent v.b. with very rudimentary branches: *counter-palisade* well-formed.

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